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A GENERIC REVIEW OF THE PLOVERS
(CHARADRIINAE, AVES)

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No. 2 — *A Generic Review of the Plovers*
(*Charadriinae, Aves*)

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For many years the relationships between the grey and golden plovers have been argued about with little agreement between the opposing schools of opinion. While there has been much discussion of the problem, a critical evaluation of the evidence supporting the maintenance of the genus "*Squatarola*" as distinct from *Pluvialis* has never been presented. With this in mind, Dr. Ernst Mayr suggested that I undertake a study of the skull morphology of the large plovers (*Pluvialis*) so that the earlier works of Lowe could be better evaluated and so that our understanding of the relationships of these species could be further clarified. Preliminary examination of some specimens and study of Lowe's papers on the anatomy and classification of the shorebirds revealed that the variations in the skull morphology and the plumage color and pattern as outlined by Lowe were not limited to *Pluvialis*, but were common to the entire subfamily. Further study of Lowe's and Peters' classification of the Charadriinae *sensu stricto* focused attention on the need for a revision of the existing generic arrangement. This need has already been pointed out by Steinbacher (1932) in his review of Lowe's major paper (1931b), and is reflected by the dissatisfaction of many workers with Peters' classification as indicated by the various, but conflicting proposals to modify his system.

Plovers have always held the interest of ornithologists from which it can be said almost *ipso facto* that many different classifications have been advanced for them. Before 1800 the species of plovers were placed in one of two large inclusive genera, *Charadrius* or *Vanellus*. The next century was characterized by the proposal of many new genera, almost to the extreme of having only one species to each genus. Seebohm, in his monumental work on the classification and distribution of the shorebirds (1888), objected to this trend toward what he considered a monotypic and impractical generic concept. In his classification, the plovers were placed in three genera, *Charadrius* (= the Charadriinae of Peters), *Vanellus* and *Lobivanellus* (= the Vanellinae of Peters).

This arrangement, although it is conservative, and the genera *Vanellus* and *Lobivanellus* are artificial, is far more acceptable than the classification in use today. With the publication of volume 24 of the "Catalogue of the Birds in the British Museum" (Sharpe, 1896), the plovers were once again divided into many genera. More importantly, Sharpe's arrangement of these genera is so unnatural that a clear idea of the generic relationships cannot be gained from study of his work. Lowe's papers on the anatomy, relationships and classification of the shorebirds, including the plovers, serve as the basis for much of the current classification of the Charadriidae *sensu lato*. Unfortunately, although Lowe did much work on the anatomy of plovers, most of his interpretations are, at best, questionable and have led to an unacceptable taxonomic arrangement. Rensch (1923), in his review of Lowe (1922), had suggested that the variation in the skull may well be modified by variations in the jaw muscles or some other factor and that there had been much parallel evolution of the skull within the plovers. The clue to a more reasonable interpretation of the skull variation has been subsequently pointed out by several German workers, but no one has yet done a complete job of checking Lowe's papers and aligning the skeletal and plumage variations with an acceptable classification of the Charadriinae *sensu lato*. Peters (1934) corrected some of Lowe's errors, mainly by shifting several misplaced genera from the Vanellinae to the Charadriinae *sensu stricto*, but in general used Lowe's conclusions as the basis for his classification, which thus still contains most of Lowe's misinterpretations. Peters' two subfamilies are natural (monophyletic) groups but they are subdivided into far too many genera. In recent years some genera, especially in the charadriine plovers, have been merged — a trend leading back to the classification of Seebohm. However, the merging has been erratic, with little agreement in the delimitation of genera, as most clearly shown in the case of *Charadrius* whose limits differ with almost every author. The merging of the charadriine genera reached its extreme limit with the recent action of the Nomenclature Committee of the British Ornithologists Union (Anonymous, 1949). This committee placed all British plovers, with the exception of *Vanellus vanellus*, into *Charadrius* without giving reasons for their action or taking

the non-British species into consideration. Even if it were correct, this type of work is unsatisfactory, for only the opinion of the several workers is presented, without the supporting evidence. Lastly, there has been no recent attempt to understand the position of the more aberrant species found in the Southern Hemisphere or the course of evolution within the subfamily.

The aims of this paper are several. Firstly, Lowe's studies on the morphology of plovers are reviewed and a new interpretation is presented in the hope that it will be in agreement with the classification of plovers here presented. Secondly, a study of the relationships and a generic classification of the plovers is advanced. This classification is based mainly on a study of external characters, of habits, habitat, and some features of the internal anatomy, chiefly the osteology. Behavior will not be used in spite of the fine work that has been done on a few species, largely because the behavior of most species is still unknown. This, however, is not to be interpreted as an attitude of undervaluation of the usefulness of comparative ethology in understanding the relationships between species of plovers, for I believe that a comparative study of their behavior may prove to be the key to clarification of the phylogeny within the large genera.

Most of the characters used in this work are those that can be seen in study skins. The original survey was done in the Museum of Comparative Zoology and supplemented by study in the American Museum of Natural History. I was able to examine all known species of plovers and most of the major plumage variations. Skeletons of a number of species were available, and those studied are listed below:

<i>Vanellus vanellus</i>	4 specimens
“ <i>coronatus</i>	2 specimens
“ <i>gregarius</i>	1 specimen
“ <i>chilensis</i>	3 specimens
“ <i>indicus</i>	2 specimens
“ <i>tricolor</i>	3 specimens
“ <i>miles</i>	2 specimens
<i>Pluvialis apricaria</i>	1 specimen
“ <i>dominica</i>	13 specimens
“ <i>squatarola</i>	29 specimens
<i>Charadrius hiaticula</i>	26 specimens
“ <i>wilsonia</i>	3 specimens
“ <i>vociferus</i>	16 specimens

Charadrius

“	<i>melodus</i>	10 specimens
“	<i>alexandrinus</i>	4 specimens
“	<i>montanus</i>	3 specimens

These specimens were examined in the collections of the American Museum of Natural History, Cornell University, and the Museum of Comparative Zoology, or borrowed from the United States National Museum, the Museum of Vertebrate Zoology at the University of California and the Museum of Natural History at the University of Kansas. In addition, a few alcoholic specimens were examined, some specimens of *Pluvialis dominica*, of *P. squatarola* and a few species of *Charadrius*. They were checked for the size and position of the nasal glands.

I am deeply indebted to Dr. Ernst Mayr who suggested the original problem, helped and guided the entire study. The officials of the Museum of Comparative Zoology and the American Museum of Natural History were most cooperative and helpful to me in the course of my work. Drs. Friedmann, Pitelka, Tordoff and Sibley kindly made available skeletons that were of great value in the study of the skull morphology. Drs. Ernst Mayr, Dean Amadon, Ernest Williams, Karl Koopmann, Daniel Marien, Robert Dressler, and Mr. Robert Risebrough have read the manuscript and offered many useful comments and suggestions for which I am most grateful. Mr. William Partridge must be thanked in particular for his help in providing information about South American plovers and for translating some important papers written in Spanish. Mr. Terrell Hamilton kindly translated von Boetticher's revision of the lapwings from the French. Miss Patricia Washer is to be credited with the fine drawings of the skull and palate.

In any taxonomic paper it is of the greatest importance to state the principles on which the proposed classification is based, but it is not necessary to outline these principles in every paper. The principles followed in this study are the same as those used in my revision of the herons (Bock, 1956). In brief, a broad concept of the genus and family is used for this is in closer agreement with the present-day species concept and results in a sounder, more easily comprehended classification.

Characters Used

Understanding of a taxonomic study depends almost entirely upon a clear presentation of the characters upon which the study is based. It is not enough to give complete and accurate diagnoses of the proposed groups because, unless he is a specialist in the group, the reader usually cannot separate the significant from the non-significant characters or understand how the characters vary. Furthermore, merely to discuss the variation of the characters is still not sufficient. To insure a full understanding of a character, it is necessary to describe and discuss its variation, its function, and how it is correlated with other structures to form character complexes. Character complexes must be treated as units, not as separate entities, for the same selection forces act on all and thus fuse them into a single evolutionary unit. When studied in this manner the selection forces acting on the character and its evolution can be more accurately examined. After the functional and phylogenetic aspects of a character have been separated and analyzed, its taxonomic value can be evaluated on a much sounder basis. The value of a systematic study is greatly increased if the taxonomic characters are evaluated in this way and, although I realize that I fall short of the goal, the characters used in classifying the plovers are presented with these ideas in mind.

The Skull

Of the several characters used by Lowe in his classification of the plovers, the skull and the color of the back were considered by him to be the most important. Eight skull characters were listed; however, only the first two were of any importance. These two characters show the most striking variation, which was "correlated" with the color of the back and upon which the classification of plovers was largely based. Since the skull characters played so large a role in Lowe's writing, I shall cite them in full and then give a brief summary of his interpretations.

In separating the genera *Pluvialis* and "*Squatarola*," Lowe lists the following skeletal characters (Lowe, 1922, pp. 478-482):

"Turning to the skull we find:

"(a) That the lacrymals in *Squatarola* are strikingly different, being

prominent out-jutting processes, almost Larine or Tringine in appearance; while in *Pluvialis* their outer margin is rounded and merged into the line of the orbital rim, being continued forwards and inwards in a smooth and somewhat noticeable convexity in a manner somewhat reminiscent of *Vanellus* (text-figs. 10b & 11b).

“(b) The interorbital space presents very distinct differences in the two forms. In *Squatarola* it is narrower both actually and relatively, while the raised corniced and everted orbital rim so characteristic of *Pluvialis* is not present; moreover, the grooves for the supra-orbital glands are not nearly so deep or defined as in *Pluvialis*, and the general arrangement here is Larine or Tringine (Text-figs. 10b & 11b). In *Squatarola* there are no anterior foramina caudad of the lacrymals. They are well marked in *Pluvialis*, and this seems to be a Charadriine character. In *Squatarola* the inner margins of the grooves for the supra-orbital glands meet in the middle line of the vertex, forming a prominent sagittal ridge down the centre. In *Pluvialis* there is a fairly broad and clearly-marked smooth medial depression down the centre of the interorbital space, which is not encroached by the supra-orbital grooves.

“(c) Turning to the palatal plates, we find in *Squatarola* that the postero-external angle is rounded off (in some specimens much cut away). In *Pluvialis* the angle is squarer.

“(d) In *Squatarola* the ectethmoid or antorbital plate is somewhat triangular in form, the extero-inferior angle representing the apex. In *Pluvialis* the antorbital plate has a quadrilateral form.” Adding in a footnote, “This, at any rate, is evident in perfectly ossified examples.”

“(e) In *Squatarola* the descending process of the lacrymal falls perpendicularly to just touch the apex of the antorbital plate. In *Pluvialis* it runs along the outer margin but does not fuse with it.

“(f) Turning to a comparison of the maxillo-palatines, we find that in the two forms under discussion these are not identical. In *Squatarola* they appear to be more closely applied to the pre-palatines, their posterior of free points being little separated from the palatal plate. In *Pluvialis* the free ends converge towards the middle line and underline the vomer, so that that part of the vomerine process is hidden when these structures are viewed from the palatal aspect. The maxillo-palatines in *Pluvialis* are also more shell-like concavo-convex structures (or more scroll-like). The attachment to the palatal process of the premaxilla is less than is *Squatarola*.

“(g) In *Squatarola* I have noticed that the dentary margin of the premaxilla is not completely fused with the corresponding portion of the maxillo-palatine as it is in *Pluvialis*. This is a Larine as opposed to Pluvialine character.

“(h) In *Squatarola* the postero-external angles of the basitemporal plate end in two fairly conspicuous downwardly projecting processes of

bone. These processes are but little evident in *Pluvialis*, but are quite characteristic of the Laridae and Sternidae. If well-prepared skeletons of the skulls of the two genera under discussion are compared, these differences are generally apparent. A similar distinction is noted between *Larus* and *Stercorarius*."

Later in the same paper (p. 483), the species of *Charadrius* were divided, on the basis of the same characteristics, into two groups, "*Leucopoliis*" (resembling "*Squatarola*") and *Charadrius* (resembling *Pluvialis*). It should be noted that not all of the species of *Charadrius* as recognized in this paper or by Peters were included by Lowe in "*Leucopoliis*" or *Charadrius*; some were placed in other genera.

The color pattern and color of the back of these genera were given (*op. cit.*, pp. 483-485) and the latter "correlated" with the skull. The light versus dark back color was said to be correlated with the degree of ossification of the supra-orbital rims (= characters "a" and "b"). Lowe considered the less ossified skull and light dorsal color primitive ("adumbrated") and the more ossified skull and dark dorsal color advanced. As he put it, the former condition was the initial attempt by nature to produce these characters and the latter was the more complete (finished) product. Thus, relationship on the horizontal level (in the same taxonomic group) is shown by skull type and back color. On the vertical axis (between ancestral and derived groups) relationship is indicated by color pattern. "*Squatarola*" and "*Leucopoliis*," in addition to a number of other forms, were combined as the "Pre-Charadriinae," a primitive group that was considered a subfamily, but never given formal status by Lowe or any subsequent author. In a later paper, Lowe (1933a) again discussed the problem of color and color pattern and here presented a list of eight "pairs" of species, set "A" being pale colored dorsally and having the skull type of "*Squatarola*," and set "B" resembling *Pluvialis* in these characters. The relationship between the 16 species is as outlined above. That is, each species or genus in set "A" (= primitive subfamily) gave rise to the corresponding species or genus in set "B" (= advanced subfamily), which assumes parallel evolution on a grand scale. Lowe speaks of some forms (his "Pre-Charadriinae") as "living fossils" (1922, p. 488; 1933a, p. 120), and believes that various groups of birds are maintained as they were in past

geological ages thus allowing ornithologists to establish phylogenetic series based on living forms. He states further (1933a, p. 114) that in the ontogenetic development of the skull of the advanced group there is a stage in the immature bird when the skull resembles that of the adult "pre-charadriine" plover. He is quite correct in his observations and indeed for a time I believed, misled by an incorrectly identified skull, that the differences between the two skull types were mainly age variations, the "pre-charadriine" condition representing the immature and the

Table 1

<i>Character complex 1</i>	<i>Character complex 2</i>
Least ossified skull Light dorsal color	More ossified skull Dark dorsal color
Ancestral (primitive)	Descendant (advanced)
"Pre-Charadriinae"	Charadriinae
" <i>Squatarola</i> "	<i>Pluvialis</i>
" <i>Leucopoliis</i> "	<i>Charadrius</i>
Set "A" (1933a) Each species or genus of the eight groups listed	Set "B" (1933a) Corresponding species or genus

The vertical columns represent the two charadriine subfamilies as delimited by Lowe. They are characterized by having a similar skull and back color. The horizontal levels show ancestral and descendant groups which are bound together by a common color pattern, the pattern being different for each group.

"charadriine" condition representing the fully ossified adult skull. This is not the case, as I discovered later. Lowe, in stating that the skull of the advanced type passed through the "primitive" stage in its ontogeny, claimed that (1933a, p. 114): "This would appear to support my conclusion that the Grey Plover and Kentish Plover are members of a group which may be regarded as antecedent in origin to, or at least more generalized than the more specialized group of which the Golden and Ringed Plovers are representatives." This is a direct application of the theory of recapitulation and as in so many other cases has led to an erroneous conclusion. Lowe always argued very strongly that these characters were not directly affected by the present day environment, but represent the condition inherited unchanged from an ancestral form. Finally, he never stated whether he considered color pattern or back color and skull type as the more important in showing relationships between genera of plovers. Table 1 summarizes Lowe's interpretations of the relationships within the plovers.

The subfamilies Vanellinae and Lobivanellinae were established by Lowe in 1922, only to be merged by him in a later paper (1931b). The main difference cited by Lowe between the Vanellinae and the Charadriinae (including the "Pre-Charadriinae") is the condition of the supraorbital rims, which in the Vanellinae are simply more ossified than in *Pluvialis*. The use of the more completely ossified nature of the supraorbital rims as the major distinguishing feature of the Vanellinae necessitated placing many obvious charadriine plovers, such as *Charadrius vociferus*, in the Vanellinae, a move to which many workers objected.

The main object in briefly summarizing Lowe's interpretations of the variations in the skull and back color in the plovers is to show that any classification based on them would be artificial. Unfortunately space does not permit a clear explanation of all the disputed points which has made the above discussion somewhat confusing. Lowe may well be right in some of his conclusions (for example, placing the turnstones in the Scolopacinae), but as so much of his work on classification and phylogeny is unsound, all of it must be reviewed before being accepted. In regard to the plovers, I was unable to accept any of Lowe's

conclusions after a careful consideration of both the evidence and other possible interpretations. The results of the present study force me to suggest that Lowe's conclusions dealing with the anatomy and phylogeny of plovers be ignored in future considerations of the relationships within the Charadriinae *sensu lato*.

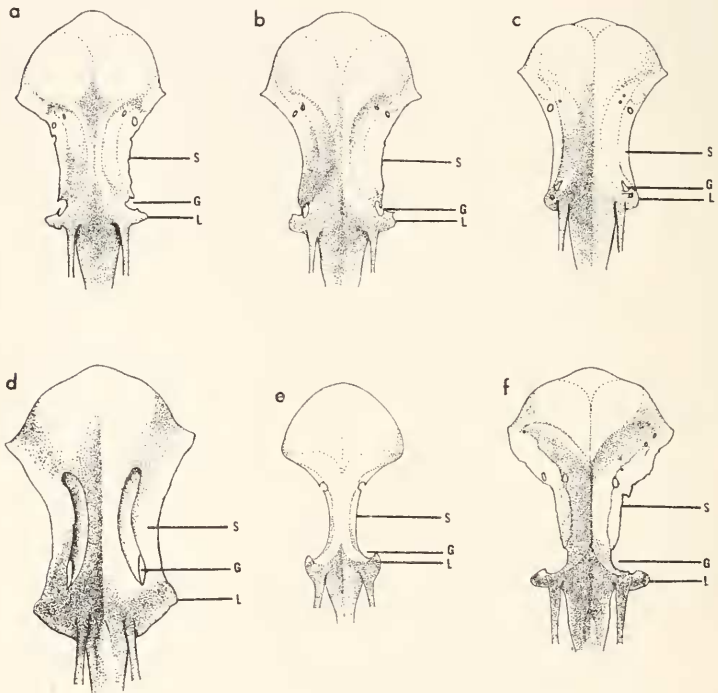


Figure 1. Dorsal view of the skull of a) immature golden plover (*Pluvialis dominica*), b) intermediate stage golden plover, c) adult golden plover, d) adult lapwing (*Vanellus vanellus*), e) adult turnstone (*Arenaria interpres*), and f) adult grey plover (*Pluvialis squatarola*) to illustrate the variation in the degree of ossification of the supraorbital rims. The labels are, from posterior to anterior, the supraorbital rims (S), the groove or foramen for the duct of the nasal gland (G), and the lacrimal bone (L). Figures are approximately life size.

Characters "a" and "b." Lowe did not describe these characters with sufficient clarity. Therefore the nature of the variation and correlation of these characters will have to be more clearly outlined before an alternative interpretation can be offered.

Examination of the differences between "*Squatarola*" and *Pluvialis* in these characters reveals that the degree of ossification of the supraorbital rims is the most important factor. In "*Squatarola*," the rims are only slightly ossified, hence the interorbital space is narrower, there is a groove, not a foramen, for the duct of the nasal gland at the anterior end of the groove in which the gland lies, and the lacrimals jut out to the sides. In the adult skull of *Pluvialis dominica*, the supraorbital rims are more fully ossified, hence the interorbital space is wider, there is a foramen, not a groove, for the duct of the nasal gland at the anterior end of the groove in which the gland lies, and the lacrimals do not jut out to the sides, but merge with the edge of the supraorbital rims in an even curve. In the lapwings, the supraorbital rims are still more ossified with small, but definite grooves for the nasal glands. Thus the interorbital space is very wide, a foramen is present for the duct of the nasal glands, and the edge of the supraorbital rims and the lacrimals merge with one another in a very smooth curve. See Figures 1f, 1c, and 1d which illustrate these structures in *Pluvialis squatarola*, *P. dominica*, and *Vanelus vanellus* respectively.

Lowe (1933a, p. 114) reported that the skull of the immature *Pluvialis dominica* ("the advanced type") passes through a stage that resembles the adult skull of the "pre-charadriine" group. My series of *dominica* fully supports this observation. The skulls of a very immature, an intermediate, and an adult golden plover are illustrated in Figures 1a, 1b, and 1c. These show an increase in the ossification of the supraorbital rims and with this, a change from the "pre-charadriine" to the "advanced" condition. Determination of the age of these skeletons is based on the total degree of ossification of the skeleton including the supraorbital rims; no skulls of known age were available. (I have only one specimen of known age, a piping plover [*Charadrius melodus*] W.B. 432 deposited at Cornell University, a bird banded as a chick and collected seven years later. The bones of this specimen, including the supraorbital rims (see Figure 2c), were completely ossified.)

When this ontogenetic change became apparent it was necessary to determine the exact nature of the fully adult (=ossified) skull of *P. squatarola*. In my series of *P. squatarola* which contained both immature and adult birds, the skulls of all specimens resembled that of the immature golden plover. It is doubtful that

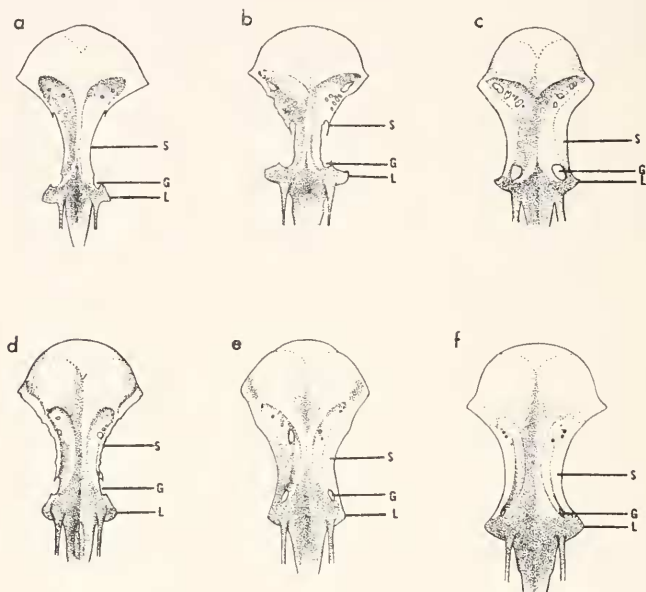


Figure 2. Dorsal view of the skull of a) adult snowy plover (*Charadrius alexandrinus*), b) adult Wilson's plover (*Charadrius wilsonia*), c) adult piping plover (*Charadrius melodus*), d) immature killdeer (*Charadrius vociferus*), e) adult killdeer, and f) adult mountain plover (*Charadrius montanus*) to illustrate the variation in the degree of ossification of the supraorbital rims. Abbreviations as in Figure 1. Figures are approximately life size.

a series of almost thirty birds collected at random over all of North America would be composed entirely of immature birds, and indeed, some specimens are certainly adults as shown by the total degree of ossification of the skeleton. It can be concluded that the adult skull of *squatarola* is similar to the very immature skull of *dominica* (see Figures 1a and 1f). The rims of the im-

mature killdeer (*Charadrius vociferus*) are less ossified than those of the adult and resemble those of the adult snowy plover (*C. alexandrinus*) or Wilson's plover (*C. wilsonia*) (see Figures 2a, 2b, 2d, and 2e). However there is no basis, as we will see more clearly later, to conclude that the skull of *squatarola* represents an ancestral type; it merely has less ossified supraorbital rims and if a species such as *P. dominica* has more fully ossified rims, it has had to pass through a *squatarola*-like stage sometime in its ontogeny — there is no alternative.

The elimination of the possibility that the differences observed are the result of comparing an immature with an adult bird necessitated an investigation of other possible factors that could influence the degree of ossification of the supraorbital rims. Since the roof of the skull is so intimately associated with the nasal (or supraorbital) glands, it would seem reasonable to try and determine whether there is a correlation between the size of these glands and the degree of ossification of the supraorbital rims. This suggestion is not new, but has been previously advanced by several German workers, who in fact have given the best possible answer to the problem of the variation in size of the nasal glands and the correlation between the size of the gland and the degree of ossification of the supraorbital rims, but the value of their work has never been fully recognized.

Schildmacher (1932), on the earlier suggestion of Heinroth, showed that in *Anas platyrhynchos* the salt content of the environment directly affected the size of the nasal glands during the life of the individual and hence the morphology of the roof of the skull. In general, the saltier the water, the larger are the nasal glands and the less ossified are the supraorbital rims and the lacrimal bones. The reason for this correlation is of no importance to us at this time, but will be discussed later; the important thing is that an inverse correlation between the size of the nasal glands and the ossification of the supraorbital rims does exist. To show this, Schildmacher conducted a simple, but conclusive experiment. He took ducklings from the same brood and reared half of them with fresh water for drinking, while the other half had salt water. At the end of a year he killed half of each group and prepared the skulls. The birds reared on fresh water had well ossified supraorbital rims and small nasal glands while the salt-water birds had poorly ossified supraorbital rims and well developed glands. These changes are clearly shown in Stresemann (1927-34, p. 52) who illustrates, after

Schiöler (1925, Danmarks Fugle, Bd. 1), the differences in the skull of the Continental European race and the Greenland race of the mallard. The remaining ducks were placed together on fresh water and at the end of the second year they were killed and their skulls prepared. This time all of the skulls were alike and resembled the skulls of the birds raised on fresh water. The changes found by Schildmacher are phenotypic and can be brought about by simply changing the salt content of the water. Schildmacher's experiments were carefully conducted with all of the necessary controls and there is no reason to doubt his results or interpretations. He points out that the supraorbital rims of the salt-water-dwelling race *Anas platyrhynchos bosacs* of Greenland are less ossified than those of the fresh-water European race *platyrhynchos*, the differences being comparable to those he obtained in his experiment. Lastly, Schildmacher reported on several eiders (*Somateria mollissima*) and a marine merganser (*Mergus serrator*) which were held on fresh water for several years. While the nasal glands did not change as much as in the case of the mallard, they did degenerate slowly in both species. It is not surprising to have a smaller change in the gland of a salt-water bird, for the nasal glands are more important to salt-water species and hence it would be advantageous to have the size of the organ more completely determined genetically and less susceptible to changes in the environment.

Technau (1936a, 1936b) studied the nasal gland in the entire class of birds. He showed that one of the functions of the secretion of the nasal glands is to protect the mucous membrane of the nasal cavity against the action of salt water.¹ With this he concluded that if, of two races of the same species or of two closely

¹ While this paper was in press, I learned of the studies of Schmidt-Nielsen and his collaborators on the function of the nasal glands of marine birds (Federation Proc., vol. 16 (1): 113-114, 1957; Amer. Journ. Physiology, April, 1958). They have shown that the nasal glands secrete (excrete) salt thereby enabling marine birds to be independent of fresh water. Schmidt-Nielsen told me (personal communication) that they have not discovered any other function of the nasal glands so that my statement of its function would be incorrect. However, the following argument of the evolution and taxonomic value of the nasal gland and associated structures is still perfectly correct with this newly discovered function of the nasal gland. Indeed, it is easier to see how the size of the gland will alter with changes in the salinity of the environment for as the amount of salt increases, the glands will have to increase in order to remove the excess salt from the body and vice versa.

related species, one were found on salt and the other on fresh water, the size of the nasal gland would differ between the two. Several cases were cited to support this conclusion, as for instance the salt-water species *Charadrius hiaticula* and the fresh-water *C. dubius* (1936b, pp. 601-603). The difference in size of the nasal glands in this species agrees with his conclusion though not as clearly as would an extreme salt-water species such as *C. alexandrinus* compared to *C. dubius*. However, the special problem of variation in the size of the nasal gland in any family was outside the scope of his study, and while Technau presented all the necessary evidence, it remained for another worker to utilize his results to solve the problem of the variation in the ossification of the supraorbital rims in the plovers.

Stegmann (1937) in a short note discussed the relationship between "*Eupoda*" (= *Charadrius*) *a. asiatica* and "*E.*" *a. veredus* which he points out are conspecific, as concluded earlier by Hartert. Yet Lowe had placed these forms in the "Pre-Charadriinae" and the Vanellinae, respectively, on the basis of skull morphology. These forms, I should add, constitute one of the pairs of species listed by Lowe in his 1933a paper. *Charadrius a. asiaticus* breeds in areas of salt deserts, *veredus* in areas of fresh water, and both winter in the interior of Africa. On the basis of this and the results of Technau's study, Stegmann concluded that the dissimilarity in the degree of ossification of the supraorbital rims was caused by a difference in the size of the nasal glands resulting from the difference in the salinity of the environment of the two species.

Lowe knew of the earlier papers on the nasal glands including Marples' (1932) discussion, but discounted the nasal glands as a possible explanation in favor of his earlier interpretation. However, Lowe's interpretation (1933a, pp. 119-129) has no factual basis and is best rejected in favor of the interpretation outlined by Technau and Stegmann.

If our hypothesis is correct, then a tabulation of the habitat and the degree of ossification of the supraorbital rims (or the shape of the skull) should show a definite correlation. What is actually being compared is the salinity of the habitat and the size of the nasal glands. The glands and the supraorbital rims change together (see below). Unfortunately a complete survey of all species cannot be made at this time for the skulls of many species are lacking in our collections as well as the much needed data on the habitat. I shall, however, outline several cases for which the necessary evidence is available.

Since this study originally started with a consideration of the grey and golden plovers, it would seem fitting to discuss them first. The golden plovers, *dominica* and *apricaria*, are predominantly fresh-water birds and have well developed supraorbital rims (Figure 1c). On the other hand, the grey plover (*squatarola*) which is predominantly a salt-water bird, has very poorly ossified rims (Figure 1f). This agrees with our hypothesis.

Of the North American species of *Charadrius*, *montanus* and *vociferus* are fresh-water birds, *wilsonia* and *alexandrinus* are the most extreme salt-water forms, and *melodus* and *hiaticula* are intermediate, but are found more on salt water than on fresh water. If the skulls of these species are compared (Figures 2a, 2b, 2e, 2e, and 2f) the close correlation between the degree of ossification of the supraorbital rims and habitat is readily apparent. The skull of *hiaticula*, which is not figured, is almost identical with that of *melodus*.

The lapwings are all strictly fresh-water birds and are even found on dry grasslands. They have the smallest nasal glands and the most ossified supraorbital rims (see Figure 1d). The close resemblance between the lapwings and some of the charadriine species such as *Charadrius vociferus*, *C. montanus*, *C. asiaticus veredus*, *Eudromias morinellus* and *E. ruficollis* (see Figures 2e and 2f), which were placed in the Vanellinae by Lowe, is due to the fact that these species are also strictly fresh-water forms and not because of any close relationship between these species and the lapwings.

The relative difference in size of the nasal glands in a fresh-water species (*Charadrius vociferus*) and a moderately salt-water species (*Charadrius hiaticula*) is shown in Figure 3.

It is thus safe to conclude that, in general, there is a strong correlation between the habitat and the shape of the skull. The species listed by Lowe in his "Pre-Charadriinae" (those with a *squatarola*-like skull) are generally salt-water birds while the species included in his "Charadriinae" (those with a *dominica*-like skull) are mainly fresh-water birds. All marine (or salt desert) species do not have one type of skull and all fresh-water-dwelling species a second type, but rather within a group, the coastal (or salt desert) species have less ossified rims

than the fresh-water-living species of that group. This point must be made because some marine species, such as *Charadrius melodus* or *C. hiaticula*, have more ossified supraorbital rims than some other marine forms such as *Pluvialis squatarola* or *Charadrius alexandrinus*.

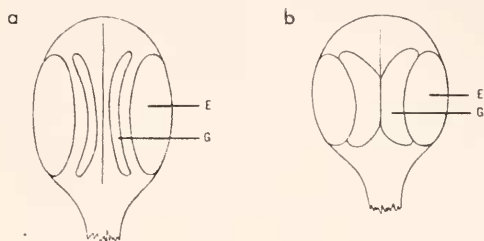


Figure 3. Diagrammatic sketch of the head of a) fresh-water plover, the killdeer, (*Charadrius vociferus*) and b) salt-water plover, ringed plover, (*Charadrius hiaticula*) to show the difference in the size of the nasal glands (G) and their relationship to the eyes (E).

One problem remains. What is the basis of the correlation between the size of the nasal glands and the degree of ossification of the supraorbital rims? Support for the glands is easily provided for by the heavy membranes present in this region in those species with poorly ossified rims — a support of bone is not needed. A number of experiments that have a direct bearing on this problem have been reported by Murray (1936) in his general treatise on bone. In the treatment of the functional changes in bone, he discusses (p. 78) the yet unexplained fact that “other pressures can cause either atrophy or at any rate limitation of growth of bone in the direction of the pressure.” Blood vessels, tendons and muscles can press against the surface of a bone and restrict growth of the bone at that point. Several experiments were cited in which the bone grew after the overlying muscle had been removed. A large nasal gland would exert a similar pressure on the bone of the supraorbital rim and in this way prevent development of bone in this region. This could be experimentally verified by a unilateral removal of the gland and examination of the skull for changes after an appropriate period

of time. This has not yet been undertaken and the basis for the correlation is still an open question.

In summary, the hypothesis is offered that the characters "a" and "b" of Lowe are affected by the size of the nasal glands and hence by the saltiness of the environment. There is a considerable mass of supporting data for this hypothesis, but it is by no means absolutely proven. A complete survey of all species to determine how well the correlation holds remains to be done. As mentioned above, this is impossible at this time because of a great lack of both skulls and habitat information for each species. A listing of the breeding and wintering grounds as well as the migration routes of each species is needed. It is also necessary to know what percentage of each species or subspecies lives on fresh or salt water, as well as whether the species breeds on fresh water and winters on the coast. An excellent example of the kind of data needed is shown by the map of the breeding and wintering grounds of the European races of *Charadrius hiaticula* in Salomonsen (1955, p. 45), who stresses the importance of the wintering area as well as the breeding grounds in understanding the selection forces that are acting on a species. Habits are important, for a bird may be strictly coastal, yet seldom go near the water, as for example *Charadrius melodus*. Knowledge of the age of the specimen is absolutely necessary because only fully adult skulls may be compared. Needless to say, a mixture of adult and immature skulls could completely obscure the picture as it did in the early stages of this investigation. It is impossible at this time to determine exactly how easily a change in the environment could change the size of the nasal gland (and also how closely the size of the nasal gland and degree of ossification of the rims are correlated), but the available evidence indicates that the selection pressure of the environment is quite strong, and if altered, it could readily change the size of the gland. This change may be genetic, non-genetic, or very likely a combination of both. It would be interesting and of the greatest value to perform the simple experiment of Schildmacher on several species of plovers. This would at least show whether the nasal glands and supraorbital rims can be phenotypically modified by the environment. Other yet unknown factors may act on this region of the skull, and must not be discounted at this time.

The variation in the amount of ossification of the supraorbital rims has provided an excellent example of an osteological feature that exhibits a very marked change as the result of a relatively minor change in the environment. The character is so readily modified that the variation in the rims has little or no value in showing generic relationships and cannot and will not be used at all in establishing the classification of plovers to be presented later in this paper. It certainly does not have the phylogenetic importance that has been ascribed to it by Lowe.

Characters "c" to "h." The remaining skull characters described above do not seem to be correlated with characters "a" and "b" or with each other and therefore will be discussed separately. A careful comparison was made only between *Pluvialis dominica* and *squatarola* which serves as the basis of the following discussions.

The "postero-external" angle of the palatines is highly variable in both species, this variation being in part natural and in part artificial, as the result of preparation. The range of variation appears, however, to overlap completely in the two species.

The ectethmoid of *squatarola* is, in general, triangular, while that of fully ossified skulls of *dominica* is quadrilateral in shape. If in *squatarola* there were a slight increase in ossification in the space between the apex of the ectethmoid and the descending process of the lacrimal, then the difference between the two species would disappear. This difference is so slight, and so well within the range of variation of the ectethmoid in *Charadrius* that it is doubtless of no generic importance.

I was unable to see any difference in the descending process of the lacrimal. In each species this process reaches the apex of the ectethmoid to touch or fuse with that bone in a similar way.

There is much variation, both individual and artificial (due to preparation), in the structure of the maxillo-palatines, but I was unable to see any constant difference between the two species.

The dentary process of the premaxillary is completely fused with the maxillo-palatine in both species. However it is entirely possible that a suture may be present in very young individuals. Any difference that may exist is most likely due strictly to variation in age.

The small process found at the "postero-external" angle of the basitemporal plate is present in both species and may be somewhat larger in *squatarola*. There is, however, a cap of tissue, probably cartilage or collagenous fibers, covering the process, which if lacking in a specimen would produce a large difference in the size of the process. The interesting feature of this process is that the internal process of the articular (medial process) of the lower jaw "articulates" on it. As the lower jaw opens, it apparently rotates on the basitemporal process as well as on the articular surfaces of the condyles of the quadrate. A full discussion of this "articulation" will be presented in a separate paper.

I have carefully checked these characters in *Pluvialis* but only briefly in *Charadrius*. However, there is no evidence to indicate that the differences as given by Lowe hold up in the latter genus. To conclude, these characters show very little difference between groups of species in *Pluvialis* or *Charadrius* and do not appear to be of value in showing relationships in those genera. Hence they will not be used in this study.

Hind Toe

The presence or absence of the hind toe has been considered by some authors to be one of the important characteristics in delimiting genera of plovers. The best example is the use of the presence of the hind toe in "*Squatarola*" as one of the major reasons for separating that genus from *Pluvialis*. It is commonly believed that, with few exceptions, all species of plovers lack the hind toe, and hence the presence of the hallux in *P. squatarola* was regarded as a very important feature. However, about half of the species of lapwings and a few charadriine plovers also have a hind toe, which fact reduces its value as a taxonomic character.

When present, the hind toe is usually very short and somewhat elevated above the plane of the remaining toes and is clearly functionless. The metatarsal for the hallux of *squatarola* is very small and free floating in the fascia of the rear of the tarsus and thus is usually lost during preparation of the skeleton. In addition, the musculature for this toe appears to have degenerated. I have dissected one specimen of this species and found what seem to be the tendons leading to the hallux. They were much

reduced but because the region was somewhat damaged, I could not determine with certainty if or how they inserted on the hallux. One specimen of *squatarola* has been reported (Brooks, 1919) to be lacking the hind toe and an extensive check of all species may well reveal more cases of a similar nature.

The reduction and eventual disappearance of a vestigial structure would be favored, as it is advantageous to inhibit the ontogenetic development of a functionless character. This simply conserves energy during embryonic development when there is rapid growth and the available energy (in terms of food) is limited. Thus if an inherited structure is not necessary to the individual during its life, its degeneration and final disappearance will be selected for, provided the proper mutations occur. The peculiar pattern of variation so characteristic of a vestigial structure results from the random occurrence of the mutations that inhibit its development. The presence or absence of a functionless structure or, when present, the variation in size or development merely demonstrates that the proper mutations have occurred in some lines and not in others.

Hence the hind toe is of no value in showing relationships in the plovers. The presence of the hallux in *Pluvialis squatarola* and its absence in its congeners probably means that the proper mutations have not yet appeared in this species and have in the others and is thus of no taxonomic value. Delacour and Mayr (1945) reached the same conclusion when they placed the grey and golden plovers in the same genus. In doing so, they say (p. 106): "Genera that are based on this loss of a morphological character are rarely valid." This conclusion has been further supported and expressed by von Boetticher (1951) for plovers and other groups, by Delacour (1951a) for woodpeckers and kingfishers, and by Mayr, Linsley and Usinger (1953, p. 122) as a general taxonomic rule. The presence or absence of the hallux has been determined and the date recorded here only to show an example of the type of variation exhibited by a vestigial structure (see Tables 2 and 3).

Wattles

Wattles are found in some species of lapwings and when present vary greatly in size, shape, and color. In general, they are

found in the space between the bill and eye and vary in size from a small disk a few millimeters in diameter to a large double wattle two centimeters long. Both sexes have wattles which are approximately the same size in each. They are usually yellow or red in color.

It has proven impossible to detect any trends in the variation of the wattles or indications that the species possessing wattles (see Table 2) are related. It is more likely that wattles have evolved and regressed independently several times in the lapwings. Thus Seebohm's arrangement of the lapwings into two groups on the basis of the presence or absence of a wattle is artificial.

At present I know of no published discussion of the functional significance of wattles in plovers. Admittedly, most of the species possessing wattles are found far from civilization, but at least one species, *Vanellus miles novaehollandiae*, occurs close to large cities in Australia and several other species can be observed in zoos. A study of the behavior of these species to determine whether wattles play a role in displays might contribute considerably to understanding their variation in the lapwings.

From their position and variation in size and color, it seems reasonable to suggest that the wattles serve as releasers associated with "courtship" or other displays or perhaps serve as species-specific recognition marks. Wattles are found in many other groups of birds, including the pheasants. The wattles in the male of *Lophura bulweri*, one of the pheasants, are used in the "courtship" displays (Delacour, 1951b, pp. 181-182). Structures used in "courtship" are peculiar in that the differences between species are generally very striking and usually do not fit into a regular pattern of variation. A more complete discussion of the problems associated with this type of character is given in the section on the plumes of herons (Bock, 1956, pp. 7-10). Delacour (1951b, p. 123) discusses the problem of wattles in the pheasants and Sibley (1957) summarizes the problem for birds in general. In brief, it should be remembered that the differences in species recognition marks are generally only of specific value, not generic.

Wing Spur

Many species of lapwings possess a spur at the bend of the wing. Where a distinct spur is lacking there is a bony knob which lies under the skin and can be felt on a study skin. The spur or knob is a bony projection on the proximal end of the carpometacarpus and varies in length from a blunt projection that does not extend beyond the feathers of the wing to a sharp spur reaching a length of two centimeters (see Rand, 1954, p. 128, for more precise figures). The spur is equally well developed in both sexes although that of the male may be a few millimeters longer. Spurs are not found in the charadriine plovers; however, there is an enlargement at the proximal end of the carpometacarpus. More precisely this process is located at the base of the alula digit and is no doubt homologous with the bony knob and spur of the lapwings. This process which in its original and also present function serves as the point of insertion of the muscle extensor metacarpi radialis provides a bony mass (knob) at the bend of the wing. As shall be shown below, this bony mass is a pre-adaptation which increases the efficiency of the wing as a weapon. The new selection force concerned with increasing the efficiency of the wing as a weapon seizes this process and developed it into a sharp spur in several species of lapwings.

The lapwing plovers are very aggressive birds especially in the breeding season. Countless reports of various species "defending" the nest or territory by flying at the intruder can be found in the literature. A picture of *Vanellus miles novaehollandiae* (Oliver, 1955, p. 270) shows the bird in a "defensive" position — crouched low with the wings half spread. The bend of the wing is one of the best weapons in birds, as so well shown by the geese and pigeons. The adult lapwing may fly at the intruder and strike it in the face or other soft part, with the wings. Nethersole-Thompson (1940) reports lapwings (*Vanellus vanellus*) attacking sheep that have strayed too close to their nest. The birds flew over the back of the sheep and struck at them with their wings. A knob or, even better, a sharp spur at the bend of the wing would increase the effectiveness of the blow that may be strong enough to startle the intruder and cause it to retreat. Lucas (1893) and Rand (1954) favor the idea that wing spurs are used for fighting (including "courtship"), citing many

groups that have spurs on the wings or that use the wing as a weapon.

Another suggestion is that the spur may have a function in the "courtship" or other displays. There are many displays in which the bird faces another individual and half raises its wings. If this additional function were demonstrated, it would in no way invalidate the first hypothesis; the spur can have both functions at the same time.

Why there is so great a variation in the development of the spur in different species of *Vanellus* is a mystery. There may well be some correlation between the habits and the length of the spur, but the habits of lapwings are unknown to such an extent that we are unable to formulate any hypothesis. Lucas suggested that the size of the spur was directly correlated with the size of the wattles; however, data presented in Table 2 shows little evidence of this correlation. The best conclusion based on the available evidence is that the presence or absence of a spur in some species of *Vanellus* is almost definitely not an indication of relationship. Most likely the spur evolved or regressed independently several times in this genus and cannot be used to group species together.

Color and Color Pattern

Color itself is usually of little importance in showing relationships between species and genera of birds. On the other hand, color pattern is often of considerable value, although generally not above the generic level. This appears to be true for the plovers.

It is well known that the back color of many (all?) species of plovers agrees with the color of the ground and serves as protective coloration. An excellent example is the piping plover (*Charadrius melodus*) which is found only on sand beaches and in color is light grey dorsally. It is usually impossible for the human observer to see the birds even though they may be calling just 100 feet away; only when they run are they easily seen. In a series of thorough studies it was shown that in the larks the color of the back is correlated with the color of the soil on which the larks live (Niethammer, 1940; Vaurie, 1951, pp. 442-446). It would be desirable to correlate in a similar manner for the

plovers the color of the soil and color of the back, but too often the color of the soil could not be determined from the literature, and to present such a table would be more guesswork than fact. However, a survey of the literature reveals numerous statements on the concealing nature of the back color. Some examples are *Vanellus coronatus* (van Someren, 1956, p. 124), *V. tricolor* (Favaloro, 1944, p. 151), *V. miles novachollandiae* (Favaloro, 1944, p. 146), *Charadrius venustus* (van Someren, 1956, p. 123), *C. tricollaris* (Haagner, 1910, p. 503), *C. modestus* (Goodall *et al.*, 1951, p. 221), *Anarhynchus frontalis* (Stead, 1932, p. 92: Oliver, 1937, p. 3), *Pluvianellus socialis* (Goodall *et al.*, 1951, p. 216), and *Eudromias ruficollis* (Goodall *et al.*, 1951, p. 208). This list could be greatly expanded, with at most a few or no cases in which the color of the back does not harmonize with the substrate. From this, we can conclude that the plovers have protectively colored backs which are under the influence of a strong and easily changed selection force (color of the ground) — a force which could alter several times during the evolution of a species or of a higher category of plovers.

In contrast to this ecotypic interpretation of back colors, Lowe (1922, p. 487; 1933a) considered the difference of a light versus dark dorsal color in the various species of *Pluvialis* and *Charadrius* to be important phylogenetically. Pale back color was thought to be primitive and to have given rise to the darker color. Furthermore, he tried to correlate the color of the back with the skull type (see above, p. 33) and asserted that the color of the back is not primarily affected by the selection forces of the present day environment. However these conclusions cannot be accepted because they were based on factual inaccuracies, as for example, the color of the back of *C. melodus* is given as darker than that of *C. alexandrinus* and the same as that of *C. hiaticula*, a statement which is quite incorrect.

The shape of the skull and the color of the back are selected for by two entirely different forces, salinity as against the color of the soil, which although they are often associated, are independent of one another. Therefore these two characters cannot be considered as correlated. If a plover lives on sandy beaches along the ocean, it will most likely have a pale colored back and a skull as illustrated for *Charadrius alexandrinus*. There is no reason

to believe, on the basis of these characters, that this species is closely related to other plovers living in the same environment and therefore having these same characteristics. Indeed, if the closest relative of the plover living on sandy coastal beaches is a species dwelling inland on muddy fields, then this species would most likely have a dark colored back and a skull as illustrated for *Charadrius vociferus*. These two sets of characters are as different as they could possibly be, yet do not invalidate the conclusion based on other characteristics that these species may be closely related. It need not be pointed out that it is a rather simple matter during the evolution of the plovers for species to shift from fresh water to salt water or from mud flats to sand beaches. Because the selection force (i.e. the environment) could easily change several times during the differentiation of two species or groups of species and because these selection forces are so powerful, I feel that certain characters, as for example the shape of the top of the skull or the color of the back, are too easily affected by the action of the environment (selected for) to be of any value in a generic revision. To say this in another way, related species may (but not necessarily) be similar in certain readily modified characters (back color and skull morphology), but those species that are similar in these characters are not necessarily related. This is in general true for any character that is under the influence of a strong selection force (= environment) which can easily change during the evolution of a group.

Pattern of coloration is usually more stable than color, for while color may change in response to a selection force, it can do so on the existing pattern. To be sure, convergence is still an important consideration because a particular selection force can select for the same pattern in unrelated birds. Usually, however, the more complex a color pattern is, the less chance there is for convergence to occur, but if a certain pattern is highly adaptive in a certain environment, it can occur in unrelated forms found in the same habitat, as shown by Friedmann (1946, p. 395).

In plovers, several color patterns are of uniform expression over large numbers of species and appear to be important in showing relationships. The head and breast markings are very constant in *Charadrius*. In *Vanellus*, the pattern of the wing

and tail is almost completely uniform in the entire genus. Here the words of Seebohm are as true today as they were in 1888 (p. vi): "I have found that in many cases the colour of such parts of the plumage as are unaffected by age, sex, or season, and which is therefore presumably of ancient origin, is apparently of much greater value in ascertaining the relationships of many birds than the so-called structural characters, which are compelled by the laws of evolution to change with the changing habits or environment of the species."

In *Charadrius* the breast bands and head markings act as disruptive marks especially when the bird is sitting on the nest. They probably also serve as species-specific releasers and this may well be the reason for their peculiar variation. Smith and Hosking in their study of *Charadrius hiaticula* point out (1955, p. 82): "It will be evident from a study of the photographs, that the Ringed Plover makes full use of the black and white patterning on its breast, chin and head, and also on its tail to produce a maximum effect of threat." Stead (1932) describes the same postures for *Charadrius bicinctus* and *Anarhynchus frontalis*. The color and color pattern of the head and breast in *Vanellus* probably also serve as releasers and species-specific recognition marks which may account for the complex and seemingly haphazard pattern of variation of these characteristics in this genus. Until more is known of the "courtship" displays of most species of plovers, especially of the lapwings, we can only assume that the differences in color pattern are important in the behavior of plovers. The forces that select for differences in these characters are so strong and varied (depending greatly upon which species are sympatric) that the resulting variation of color pattern has largely obscured the relationships between species. Thus while color pattern is very valuable in allying large groups of species, the variation within each pattern can be used only with the greatest caution to show relationships in *Charadrius*, and even less in *Vanellus*.

Osteology

The skeletons of some species of plovers (see above, p. 29) were compared primarily to see if there were any characters that separated the lapwings from the charadriine plovers, and

secondly to see if there were any differences between *Charadrius* and *Pluvialis*. A complete study was not done as the skeletons of relatively few species were readily available and an examination of these specimens indicated that it would not be practical to borrow the necessary material for a thorough investigation at this time.

In brief, the plovers seem to be a very homogeneous group osteologically. In the skull the most striking difference is the contour of the roof which has already been discussed in detail (see p. 31). The size and shape of the ectethmoid varies, especially in *Charadrius*, and may well be correlated with the size of the bill, but it is not known what possible taxonomic implications it may have. Rensch (1923, p. 69) suggested that the outline of the foramen magnum differs between *Charadrius* and *Pluvialis*, that of *Charadrius* being more oblong, that of *Pluvialis* rounder. I have examined skulls of *P. dominica* and *P. squatarola* and the North American species of *Charadrius* for this character. In general, Rensch's observations were confirmed, but some variation exists in *Charadrius* and until this is more fully investigated, the value of the foramen magnum as a diagnostic character cannot be determined.

The limb bones as well as the trunk skeleton were compared with equally negative results. The proximal end of the tarsometatarsus may differ between *Pluvialis* and *Charadrius*. In *Charadrius* there appear to be more canals in the hypotarsus for the passage of tendons than in *Pluvialis*, but not enough species have been studied to be sure that this is a constant difference.

To conclude, I have been unable, after a brief survey, to discover any osteological characters that proved to be useful in understanding the relationships within the plovers. However, some of the characteristics such as the shape of the foramen magnum or the configuration of the canals of the hypotarsus may prove to be valuable with further study. Because the plovers are a very homogeneous group, if a comparative study of their osteology is done in hopes of finding additional clues to relationships, large series of skeletons will be needed in addition to a good representation of species to be certain that individual and age variations are distinguished from the true differences between genera.

No other anatomical systems were studied.

The Position of the Charadriinae

A study of the status and taxonomic ranking of the plovers as a group is beyond the scope of this paper. However, because opinions on the relationships and status of the plovers differ so greatly, a brief summary of the problem should be given. The plovers were considered as a subfamily of the Charadriidae (which included most of the birds known as the "shorebirds") in the important works of Seebohm, Fürbringer, Gadow, Beddard and more recently by Stresemann and by Mayr and Amadon. On the other hand, Sharpe, Ridgway, Lowe, Peters and Wetmore separated the plovers as a distinct family (perhaps including such genera as *Haematopus*), which is currently the more widely accepted view.

The present trend toward a broad concept of taxonomic categories has more promise for a sounder, more rational classification of birds than the existing one which is based on the theory that morphological differences, no matter what they are, require taxonomic separation. In the proposed classification, most of the formerly recognized genera are merged and the close relationship between the remaining genera is emphasized. Hence there is no longer any need for maintaining family status for the plovers or the two subfamilies as currently used. The most consistent classification is to include the plovers as a subfamily of an enlarged family of shorebirds. The classification of Mayr and Amadon (1951) will be accepted for the purposes of this paper and the usage of family and subfamily names will follow their terminology.

Some difficulty may arise in the discussions over the exact meaning of the family and subfamily names. In the event of any possible confusion, the following convention will be adopted. When the names Charadriidae or Charadriinae are used in the sense of Mayr and Amadon they will not be qualified or they will be followed by *sensu lato*, and when they are used in the sense of Peters, they will be followed by *sensu stricto*.

The limits of the Charadriinae and a description of the subfamily are somewhat difficult to give largely because of the uncertain position of the genera *Arenaria* and *Aphriza* (the turnstones and surfbirds) and to a lesser extent, *Phegornis* and *Peltohyas*. A full discussion of each group will be presented

below. Most important is that, with the possible exception of these four genera, all of the species included in the Charadriinae in this study are more closely related to each other than to any other genus of the Charadriidae. If future study should prove that any of these four problem genera are indeed to be included in the Charadriinae, they would almost certainly constitute a group(s) separate from the genera included in the Charadriinae in this study.

The plovers comprise a single subfamily of the Charadriidae with no formal groups recognized between the subfamily and generic levels. A good diagnostic description for the plovers has not been given in any of the standard works on the anatomy and classification of birds. However, within the plovers, the largest gap exists between the lapwings (*Vanellus*) and the genera of charadriine plovers (*Pluvialis*, *Charadrius*, *Anarhynchus*, *Eudromias* and *Pluvianellus*). The charadriine plovers form a very closely knit group with only slight gaps between the genera. While these gaps are small, they are larger than the gaps between the congeneric species which merge into one another in many characteristics. Essentially there is a large genus, *Charadrius*, with a very closely allied genus, *Anarhynchus*, and three small outlying genera, *Pluvialis*, *Eudromias* and *Pluvianellus*. If the proposal of the Nomenclature Committee of the British Ornithologists Union (Anonymous, 1949) is followed, then all of the charadriinae plovers must be placed in *Charadrius*; there is no other alternative. This is not an unreasonable course of action and may even be the best, but at present I feel that it would be too inconsistent with the current concepts of avian taxonomy and prefer to maintain the several genera of charadriine plovers as proposed in this paper.

The following arrangement of genera and species attempts to show relationships as based on a comparative study of the characters described above. It would be desirable to group the genera and species in some definite sequence, say from the most primitive to the most specialized form in each category. Unfortunately, however, I have been most unsuccessful in discovering what is primitive and what is specialized, so that the linear arrangement is mainly for convenience and is admittedly partly artificial. Superspecies (for definition, see Mayr, *et al.*, 1953.

p. 29) are bracketed. Whenever a species has been transferred to a new genus, the old generic name (Peters' classification of 1934 is used as the basis of comparison) follows in parenthesis.

Classification of the Charadriinae

Genus *Vanellus*

- vanellus*
- crassirostris* (*Hemiparra*)
- { *armatus* (*Hoplopterus*)
- { *spinosus* (*Hoplopterus*)
- { *duvaucelii* (*Hoplopterus*)
- tectus* (*Sarciophorus*)
- malabaricus* (*Lobiptuvia*)
- albiceps* (*Xiphidiopterus*)
- lugubris* (*Stephanibyx*)
- melanopterus* (*Stephanibyx*)
- coronatus* (*Stephanibyx*)
- senegallus* (*Afribyxx*)
- melanocephalus* (*Tylibyx*)
- superciliosus* (*Anomalophrys*)
- gregarius* (*Chettusia*)
- leucurus* (*Chettusia*)
- cayanus* (*Hoploxypterus*)
- chilensis* (*Belonopterus*)
- resplendens* (*Ptiloscelys*)
- cinereus* (*Microsarcops*)
- indicus* (*Lobivanellus*)
- macropterus* (*Rogibyxx*)
- tricolor* (*Zonifer*)
- miles* (*Lobibyxx*) includes
novae-hollandiae

Genus *Pluvialis*

- { *apricaria*
- { *dominica*
- squatarola* (*Squatarola*)
- obscura* (*Pluviorhynchus*)

Genus *Charadrius*

- { *hiaticula*
- { *placidus*
- dubius*
- wilsonia*
- vociferus*
- melodus*
- thoracicus*
- pecuarius*
- tricollaris*
- alexandrinus*
- peronii*
- venustus*
- collaris*
- { *bicinctus*
- { *falklandicus*
- { *mongolus*
- { *leschenaultii*
- { *asiaticus* (*Eupoda*)
- { *modestus* (*Zonibyxx*)
- montanus* (*Eupoda*)
- melanops* (*Euseyornis*)
- cinctus* (*Erythrogonys*)
- rubricollis*
- novae-zeelandiae* (*Thinornis*)

Genus *Anarhynchus*

frontalis

Genus *Eudromias*

- morinellus*
- ruficollis* (*Oreopholus*)

Genus *Pluvianellus*

socialis

Genera = 6

Species = 56

Incertae sedis

Genus <i>Phegornis</i> (=Scolopacinae †, see p. 80) <i>mitchellii</i>	Genus <i>Aphriza</i> (=Scolopacinae †, see p. 85) <i>virgata</i>
Genus <i>Peltohyas</i> (=Glareolidae †, see p. 84) <i>australis</i>	Genus <i>Arenaria</i> (=Scolopacinae †, see p. 85) <i>interpres</i> <i>melanocephala</i>

Genera recognized by Peters and synonymized here are:

<i>Afribyx</i> = <i>Vanellus</i>	<i>Microsarcops</i> = <i>Vanellus</i>
<i>Anomalophrys</i> = <i>Vanellus</i>	<i>Oreopholus</i> = <i>Eudromias</i>
<i>Belonopterus</i> = <i>Vanellus</i>	<i>Pluviorhynchus</i> = <i>Pluvialis</i>
<i>Chettusia</i> = <i>Vanellus</i>	<i>Ptiloscelys</i> = <i>Vanellus</i>
<i>Elseyornis</i> = <i>Charadrius</i>	<i>Rogibyx</i> = <i>Vanellus</i>
<i>Erythrogonys</i> = <i>Charadrius</i>	<i>Sarciophorus</i> = <i>Vanellus</i>
<i>Eupoda</i> = <i>Charadrius</i>	<i>Squatarola</i> = <i>Pluvialis</i>
<i>Hemiparra</i> = <i>Vanellus</i>	<i>Stephanibyx</i> = <i>Vanellus</i>
<i>Hoplopterus</i> = <i>Vanellus</i>	<i>Thinornis</i> = <i>Charadrius</i>
<i>Hoploxypterus</i> = <i>Vanellus</i>	<i>Tylibyx</i> = <i>Vanellus</i>
<i>Lobibyx</i> = <i>Vanellus</i>	<i>Xiphidiopterus</i> = <i>Vanellus</i>
<i>Lobipluvia</i> = <i>Vanellus</i>	<i>Zonibyx</i> = <i>Charadrius</i>
<i>Lobivanellus</i> = <i>Vanellus</i>	<i>Zonifer</i> = <i>Vanellus</i>

The following species, accepted by Peters, have been reduced to subspecific status or synonymized (see under the respective genera):

<i>Charadrius alticola</i> = <i>C. falklandicus alticola</i>
<i>Charadrius sanctaehelenae</i> = <i>C. pecuarius sanctaehelenae</i>
<i>Eupoda veredus</i> = <i>Charadrius asiaticus veredus</i>
<i>Lobibyx novaehollandiae</i> = <i>Vanellus miles novaehollandiae</i>
<i>Rogibyx tricolor</i> = <i>Vanellus macropterus</i>

In the generic headings that follow, the generic name is followed by the describer's name, then the type species follows in parenthesis, and finally the year in which the genus was described. The included species are listed and a brief generic synonymy is given. For a more complete synonymy, the reader is referred to the standard works of Sharpe, Ridgway, Peters, and Hellmayr and Conover. The ranges are taken chiefly from Peters.

VANELLUS BRISSON (*VANELLUS*) 1760

Synonymy: *Hoplopterus* Bonaparte, 1831 (*spinosus*); *Chettusia* Bonaparte, 1841 (*gregarius*); *Lobivanellus* Strickland, 1841 (*spinosus*); *Sarciopterus* Strickland, 1841 (*tectus*); *Cranellus* Tobias, 1844 (*spinosus*); *Vanellochettusia* Brandt, 1852 (*leucurus*); *Belonopterus* Reichenbach, 1852 (*chilensis*); *Tylibyx* Reichenbach, 1852 (*melanocephalus*); *Sarcogrammus* Reichenbach, 1852 (*indicus*); *Xiphidiopterus* Reichenbach, 1852 (*albiceps*); *Stephanibyx* Reichenbach, 1852 (*coronatus*); *Hoploxypterus* Bonaparte, 1856 (*cayanus*); *Ptiloscelys* Bonaparte, 1856 (*resplendens*); *Lobipluvia* Bonaparte, 1856 (*malabaricus*); *Diflippia* Salavadori, 1865 (*crassirostris*); *Hemiparra* Salavadori, 1865 (*crassirostris*); *Limmetes* deFilippi, 1870 (*crassirostris*); *Nomusia* Heuglin, 1877 (*crassirostris*); *Lobibyx* Heine, 1890 (*novaeollandiae* = *miles*); *Microsarcopterus* Sharpe 1896 (*cinereus*); *Eurypterus* Sharpe, 1896 (*leucurus*); *Zonifer* Sharpe, 1896 (*tricolor*); *Anomalophrys* Sharpe, 1896 (*superciliosus*); *Euhyas* Sharpe, 1896 (*leucurus*); *Zapterus* Oberholser, 1899 (*leucurus*); *Rogibyx* Mathews, 1913 (*tricolor* = *macropterus*); *Afribyx* Mathews, 1913 (*sengallus*); *Titihouia* Roberts, 1924 (*melanopterus*).

Included Species: *vanellus*, *crassirostris*, *armatus*, *spinosus*, *duvaucelii*, *tectus*, *malabaricus*, *albiceps*, *lugubris*, *melanopterus*, *coronatus*, *senegallus*, *melanocephalus*, *superciliosus*, *gregarius*, *leucurus*, *cayanus*, *chilensis*, *resplendens*, *cinereus*, *indicus*, *macropterus*, *tricolor*, and *miles*.

Diagnosis: When the color and pattern of the body plumage are considered, the lapwings are a very diverse group, but there is a common tail and wing pattern that ties the species together. The tail (except for *leucurus*, which has an all-white tail) is white basally with a broad black band on the distal half and often with a narrow white terminal band. The primaries are

always black and generally (except for *vanellus* and *miles* which have a unicolored wing) marked by a broad wing stripe that

Table 2

Species	Hind Toe	Wing spur	Wattles		Habitat
			size	color	
<i>vanellus</i>	+	—	—	—	marshes
<i>crassirostris</i>	+	—	—	—	streams, lakes
<i>armatus</i>	—	+(9-12mm)	—	—	grasslands, flats near water
<i>spinosus</i>	—	+(5-11mm)	—	—	fields near water
<i>duvaucelii</i>	—	+(11-13mm)	—	—	marshes, rivers
<i>tectus</i>	—	—	1, large	crimson	dry grasslands
<i>malabaricus</i>	—	—	2, large	yellow	dry grasslands
<i>albieeps</i>	—	+(18-23mm)	1, large	greenish yellow	marshes, streams
<i>lugubris</i>	—	—	—	—	dry grasslands
<i>melanopterus</i>	—	—	—	—	dry grasslands
<i>coronatus</i>	—	—	—	—	dry grasslands
<i>senegallus</i>	+	+(3-11mm)	2, large	red and yellow	marshes, dry fields
<i>melanocephalus</i>	+	—	1, small	red	marshes
<i>superciliosus</i>	—	—	1, small	yellow	dry grasslands
<i>gregarius</i>	+	—	—	—	marshes
<i>leucurus</i>	+	—	—	—	grasslands, marshes
<i>cayanus</i>	—	+(4-9mm)	—	—	marshes, streams
<i>chilensis</i>	+	+(8-14mm)	—	—	marshes
<i>resplendens</i>	—	—	—	—	mountain streams
<i>cinereus</i>	+	—	1, small	yellow	marshes
<i>indicus</i>	+	—	1, small	red	marshes, dry fields
<i>macropterus</i>	+	+(15mm)	2, large	pink and white	?
<i>tricolor</i>	—	—	1, small	red	fields
<i>miles</i>	+	+(15-17mm)	2, large	yellow	marshes

Variation of several characters in *Vanellus*. If the characteristic is present in a species, it is symbolized by a +, if absent, by a —. Under wing spur the figures following the + are the lengths of the spur given by Rand; a — means that a knob rather than a fully developed spur is present.

begins on the greater coverts of the primaries and extends diagonally across the secondary coverts and the secondaries themselves so that in some species the innermost secondaries are completely white. Such features as the head and breast pattern, and presence and size of the wattles and wing spur vary from species to species and probably serve as releasers in connection with species-specific behavior displays and hence are specific, not generic characters. In habitat, the lapwings are all inland birds, found on dry grasslands or barrens, marshes, swamps or the edges of streams and rivers. They are noisy birds, constantly flying around an intruder and calling loudly, much more so than the charadriine plovers.

Range: World-wide except for North America. The center of distribution is Africa and, to a lesser extent, southern Asia.

Remarks: Compared to Peters' treatment of the lapwings, the proposal to place the lapwings in a single genus seems at first to be very radical. Yet if we compare the merits of the two arrangements, the greater usefulness of the present proposal should become apparent. In Peters' classification, the 25 species of lapwings are placed in 19 genera of which only *Stephanibyx* and perhaps *Chettusia* contain more than a single superspecies — a classification in which almost every genus is monotypic. If, on the other hand, the lapwings are regarded as congeneric, the result will be a single genus of 24 (or 25) species. By the standards of avian taxonomy this is a large genus, but no more so than many others such as *Buteo* (27 species), *Corvus* (32), *Accipiter* (33), *Larus* (35), *Anas* (36), *Falco* (37), *Caprimulgus* (39), *Dicaeum* (41) and *Turdus* (63). These genera are characteristically highly successful groups which have undergone an extensive adaptive radiation to produce the large and complex groups we know today. A serious attempt has been made to discover divisions within the lapwings that could be considered as genera, but at best only poorly marked trends of certain characters could be determined — no clearly separated groups of species could be found. We are thus faced with accepting either Peters' arrangement or placing the lapwings in a single genus; at present there seems to be no other alternative. If the broad limits of *Charadrius* are accepted, and as the other alter-

native is a relatively useless monotypic generic classification, there should be little doubt that the most reasonable action is to place all of the species of lapwings in *Vanellus*, as proposed in this paper.

White (1952) and more recently von Boetticher (1954) have studied the relationships of the lapwings and attempted to synonymize some of the small genera. White quite correctly pointed out that the characters on which the old genera were based (presence or absence of the hallux and scutellation of the tarsus) were of little taxonomic value. He then based his relationships on the nature of the wattles and the wing spur. Von Boetticher used the presence (including the relative development) or absence of the hind toe, of the wattles and of the wing spur as the major characters in establishing his genera. As has already been shown in this paper, all of these characters do not appear to have any value in determining generic relationships. Thus, while these works have merit as attempts to understand the relationships within the lapwings, the genera proposed by these authors are with little doubt artificial and therefore cannot be accepted.

Merely to place the lapwings in a single genus is of no more help in understanding their relationships than to place each species in a separate genus. I have tried, but with little success, to sort out subgroups or trends within the lapwings. It is doubtful that the problem of relationships between the species of *Vanellus* can ever be solved by a study, no matter how intensive, of museum skins or of the internal anatomy because the characteristics seen on the the skins are subject to strong and variable selection forces while the internal anatomy is too uniform. Rather, solution of this problem will probably be through an investigation of comparative behavior or perhaps serology and similar studies. Several subgroups, however, do separate out and these will be presented as the best possible arrangement for the present. The characters supporting these groups are very vague and best serve to illustrate the extreme difficulty of the problem and the weakness of the suggested arrangement. The relationships and a rough indication of the distribution of the lapwings are illustrated in Figure 4.

Africa, the center of distribution for the genus, is the home of

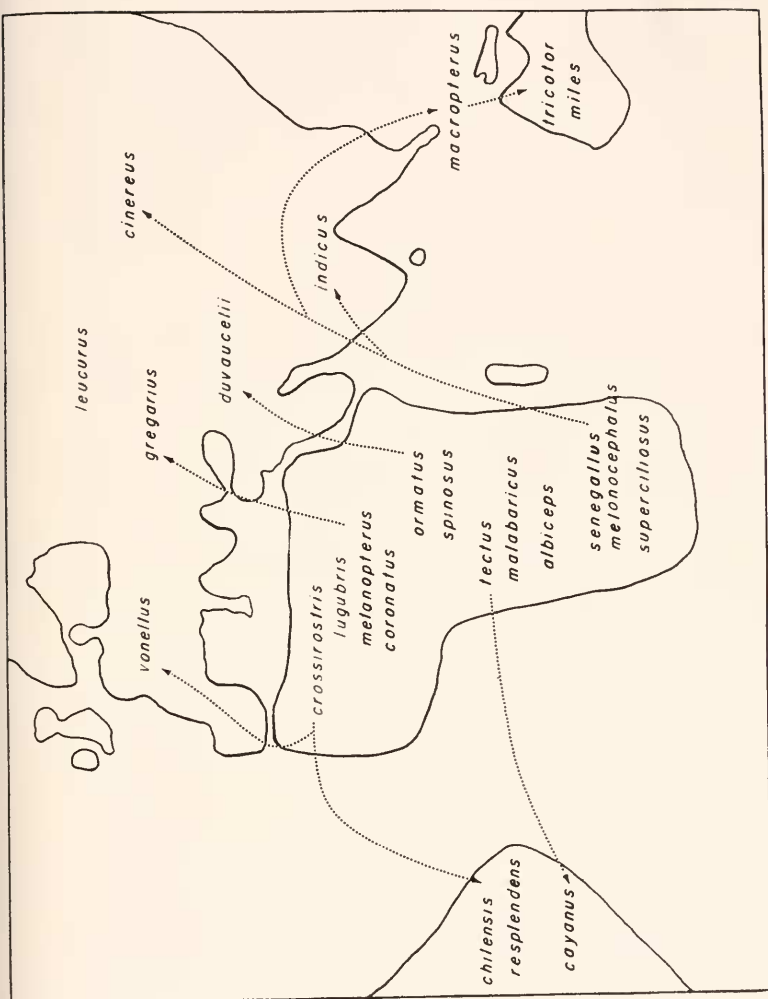


Figure 4. Diagram showing the relationships within *Vanellus*. The species are placed in the continent in which they breed. Relationships between groups and the probable routes of dispersal are shown by the dotted lines. See the text for a discussion of the relationships within the lapwings.

the largest species group, namely *crassirostris*, the *armatus-spinosus-duvaucelii* (Asiatic) complex, *tectus*, *malabaricus*, *albiceps* and the *lugubris-melanopterus-coronatus* complex. The characters shared by these species are hard to define, but the wing pattern is somewhat similar in all of them and there are some general similarities in the head and breast pattern. The European *vanellus* is probably an offshoot of this group.

The species *senegallus* and *melanocephalus* may well be related to one another as they are the only lapwings with streaking on the throat. They are similar to the first group in wing pattern and coloration of the throat and may be considered as a branch of that group.

The small *superciliosus* is quite different from the other lapwings in that the color of the breast is red (unique in this genus), and the fact that it lacks the head markings found in many of the other species. At present it is impossible to point to any species as its closest relative.

The two species found in central Asia, *gregarius* and *leucurus*, may be related to *coronatus* of Africa. The breast and head pattern of *gregarius* is similar to that of *coronatus*. The close similarity between *gregarius* and *leucurus* makes it reasonably clear that they diverged from a common ancestor after it had become established in Asia.

The South American *cayanus* appears to be derived from the large African group, but again it is impossible to point to any species as its closest relative. It has a breast band and head pattern like some of the African species, but the coloration of the back is quite unique. The brown of the center of the back is bordered by white while the scapulars are black, a pattern that is found nowhere else in the lapwings.

The other two species of South American lapwings, *chilensis* and *resplendens* are closely related to one another and represent an invasion of South America separate from *cayanus*. The back of each species is a metallic greenish color similar to that of *vanellus*. In addition, *chilensis* possesses a head tuft and black breast band like those of *vanellus*. These species are certainly closest to *vanellus*.

The complex consisting of *cinereus*, *indicus*, *macropterus*, *tricolor*, and *miles* (including *novachollandiae*) constitute the Far Eastern and Australian lapwings. Except for *cinereus*, all have

a black crown and some black on the breast. The back of all species is brown, all have wattles and generally a fainter wing bar than their congeners. They seem to be closest to some of the species of the large African group, perhaps *melanopterus* or *albiceps*.

It can now be appreciated why I consider the evidence supporting the delimitation of these groups as very poor. The above arrangement has to a large extent divided the lapwings into groups according to their geographic occurrence. This may convey the impression that there has been a small radiation in each of these regions, which probably is not the case. What seems to be more likely is that Africa was the center of diversification and the species have spread from there. There is little doubt that there have been two separate invasions of South America. Asia and Europe were invaded from Africa by at least five different lines, *vanellus*, *gregarius*, *cinereus*, *indicus* (giving rise to the other Far East and Australian species?), and *duvaucelii*, and there may have been more (some of the other Far East and Australian species).

The ranges of *miles* and *novachollandiae* as given in the literature appear to be allopatric. The major differences between these forms are an extension of the black crown down the hind neck and sides of the breast in *novachollandiae* and a difference in the wattles and body size. They are similar in all other features and as their ranges seem to be allopatric, it is assumed in this paper that they are conspecific. However, there is still doubt as to whether or not the ranges of these forms overlap in Queensland and if they do, *miles* and *novachollandiae* must be regarded as distinct species, and in that case would constitute a super-species.

The three species of the former genus *Hoplopterus* — *spinosus*, *armatus* and *duvaucelii* — are all allopatric. The ranges of *armatus* and *spinosus* come close to one another and some authors (Mackworth-Pread and Grant, 1952, pp. 357-358) show their ranges overlapping in Kenya, but a careful survey of the literature indicates that there is no overlap in breeding range (Jackson, 1938, pp. 354-355). While the color pattern of the three species is similar, there are a number of plumage differences which make the species strikingly dissimilar so it is likely that if the ranges did overlap, individuals of the several species would

avoid one another and thus prevent mixed pair formation and interbreeding. No intermediates between the species have ever been reported, nor is there any indication of trends in one species toward another. Hence they are best considered as distinct species, but as their ranges are allopatric, they form a superspecies.

Zonifer tricolor of Australia was described by Vieillot in 1818 several years before Horsfield described *Rogibyx tricolor* of Java in 1821. Since these two species are now placed in the same genus, a name must be substituted for *Rogibyx tricolor*. The next available name for the Java bird is *macropterus* Wagler, which was published in the combination *Charadrius macropterus* in Wagler's *Systema Avium* (1827, p. 77, species 54).

PLUVIALIS BRISSON (APRICARIA) 1760

Synonymy: *Squatarola* Cuvier, 1817 (*squatarola*); *Pluviorhynchus* Bonaparte, 1856 (*obscura*).

Included species: *apricaria*, *dominica*, *squatarola* and *obscura*.

Diagnosis: The back of these large chunky plovers is mottled brown or grey (less so in *obscura*) while the underparts are uniformly black or reddish brown (*obscura*) in color. There may or may not be a wing stripe or white patch on the rump and tail. The conspicuous color of the underparts is lost in the post-nuptial molt and replaced by a greyish or tan color. The immature is similar in color to the adult in the non-breeding plumage.

Range: Breeds in the Arctic tundra south to Central Europe, migrates and winters south to southern Africa, South America and Australia. *Pluvialis obscura* is found only in New Zealand.

Remarks: I have shown in another part of this paper (see above, p. 31) that the characters used to separate *Squatarola* from *Pluvialis*, mainly the structure of the skull and the presence of a hind toe in *Squatarola*, are of no help in showing relationships or differences on the generic level. The two forms are so nearly identical in all respects that there should be no doubt that they are congeneric. There is a greater difference between *obscura* and its congeners. Its back is only faintly mottled in addition to its underparts being reddish, not black in color. Compared to the large number of similarities in color pattern and body size and shape, the differences in the color of the back

Table 3

Species	Hind Toe	Breast bands		Back color	Range
		number	color		
<i>Pluvialis</i>					
<i>apricaria</i>	—	—	black	brown	} Holartic
<i>dominica</i>	—	—	black	brown	
<i>squatarola</i>	+	—	black	light grey	Holartic
<i>obscura</i>	—	—	reddish brown	brown	New Zealand
<i>Charadrius</i>					
<i>hiaticula</i>	—	1, complete	black	brown	Holartic
<i>placidus</i>	—	1, complete	black	brown	Eastern Asia
<i>dubius</i>	—	1, complete	black	brown	Old World
<i>wilsonia</i>	—	1, complete	black	brown	New World
<i>vociferus</i>	—	2, complete	black	brown	New World
<i>melodus</i>	—	1, incom., or complete	black	light grey	North America
<i>thoracicus</i>	—	1, complete	black	brown	Madagascar
<i>pecuarius</i>	—	—	white	brown	Africa
<i>tricoloris</i>	—	2, complete	black	brown	Africa
<i>alexandrinus</i>	—	1, incom.	black	light brown to grey	World-wide
<i>peronii</i>	—	1, incom.	♂, black ♀, red	pale brown	East Indies
<i>venustus</i>	—	1, complete	red	light grey	Africa
<i>collaris</i>	—	1, complete	black	brown	South and Middle America
<i>bicinctus</i>	—	2, complete	upper black lower red	brown	New Zealand
<i>falklandicus</i>	—	2, complete	black	brown	South America
<i>mongolus</i>	—	1, complete	rufous	brown	Asia
<i>leschenaultii</i>	—	1, complete	rufous	brown	Asia
<i>asiaticus</i>	—	—	reddish	brown	Asia
<i>modestus</i>	+	—	reddish	brown	South America
<i>montanus</i>	—	—	tan	brown	North America
<i>melanops</i>	—	1, complete	black	brown	Australia
<i>cinctus</i>	+	1, complete	black	brown	Australia
<i>rubricollis</i>	—	1, incom.	black	pale brown	Australia
<i>novaeeseelandiae</i>	—	—	white	brown	New Zealand

Table 3 (Continued)

Species	Hind Toe	Breast Bands		Back Color	Range
		Number	Color		
<i>Anarhynchus</i> <i>frontalis</i>	—	1, complete	black	grey	New Zealand
<i>Eudromias</i> <i>morinellus</i>	—	—	rufous	grey-brown	Palearctic
<i>ruficollis</i>	—	—	grey	brown	South America
<i>Pluvianellus</i> <i>socialis</i>	+	1, diffuse	grey	grey	South America

Variation of several characters in the charadriine plovers. As in Table 2, a + indicates that the character is present; — indicates absence of the character. Under the heading of breast bands, incomplete means that the band is not continuous around the breast. If the breast band is absent, the color of the breast is given, otherwise the color of the band is given.

and reddish brown breast lose much of their importance. This is supported by the condition in *Charadrius* where the color of the breast bands may be black or rufous in closely allied species or even in the same species. The habits of *obscura* are much like those of *dominica* (Robson, 1884).

The two species of golden plovers (*dominica* and *apricaria*) are very similar to one another and their ranges are almost completely allopatric. All of the major works on Palearctic birds state that the ranges of the two overlap in the region of the Yenisei River in Western Siberia (Popham, 1897, p. 192, Dementiev and Gladkov, 1951, pp. 40, 47); hence the two forms must be considered as distinct species. As the amount of overlap is so slight and the two species are so similar, their relationship to one another is best shown if they are placed in the same super-species, as has been concluded by Delacour and Mayr (1945, p. 106). The closeness of this relationship is further supported by the report of an apparent hybrid between the two species (Popham, 1900).

CHARADRIUS Linnaeus (HIATICULA) 1758

Synonymy: *Erythrogonys* Gould, 1838 (*cinctus*); *Eupoda* J. F. Brandt, 1845 (*asiaticus*); *Thinornis* G. R. Gray, 1845 (*novaezeelandiac*); *Zonibyr* Reichenbach, 1852 (*modestus*); *Podasocys* Coues, 1866 (*monta-*

nus); *Eupodella* Mathews, 1913 (*veredus* = *asiaticus*); *Elseya* Mathews, 1913 (*melanops*); *Elseyornis* Mathews, 1914 (*melanops*); See Peters, 1934, pp. 245-246 for complete synonymy.

Included species: hiaticula, placidus, dubius, wilsonia, vociferus, melodus, thoracicus, pecuarius, tricollaris, alexandrinus, peronii, venustus, collaris, bicinctus, falklandicus, mongolus, leschenaultii, asiaticus, montanus, melanops, cinctus, rubicollis, and novaezeelandiae.

Diagnosis: Small to medium sized plovers, usually with a heavy breast band or a black forehead and black line connecting the bill and the eye, or both. This very characteristic breast and head pattern, so well illustrated in *hiaticula*, is found in a more or less developed state throughout the genus. In the superspecies *asiaticus-modestus* these markings have largely disappeared, but the last remnants can still be seen. The pectoral bands may be single or double; often they are incomplete around the breast and exist only as a vertical bar on the shoulder or may be completely absent. The breast band is usually black but may be reddish or rufous. In one species, *peronii*, the male has a complete black band while in the female the band is rufous and incomplete. In a few species the black breast band is complete around the back. More commonly, however, there is a complete white collar on the hind neck which separates the brown or grey crown from the back. The back is dark brown to pale grey in color. Underparts are usually white except for the breast bands, but in a few species, such as *modestus*, the breast may be reddish in color. A white wing stripe may be present or absent. The central tail feathers are dark brown or grey according to the color of the back while the lateral feathers are white. In a few species such as *vociferus* the tail pattern has become elaborate. Most species have little or no sexual or seasonal variation in plumage and the immature is similar to the adult.

Range: World-wide.

Remarks: Except for the addition of several somewhat aberrant species, Peters' delimitation of the genus *Charadrius* is followed in this paper. Like *Vanellus*, the genus is large and complex and the path to understanding the relationships between the species is full of pitfalls. My attempts to arrange the species in a natural order and to discover the relationships between them have met with only limited success because of the

nature of the characters used. The color of the back is strongly selected for as concealing coloration and, contrary to Lowe's claims, is of little use in showing relationships. The number, development and color of the breast bands and head markings

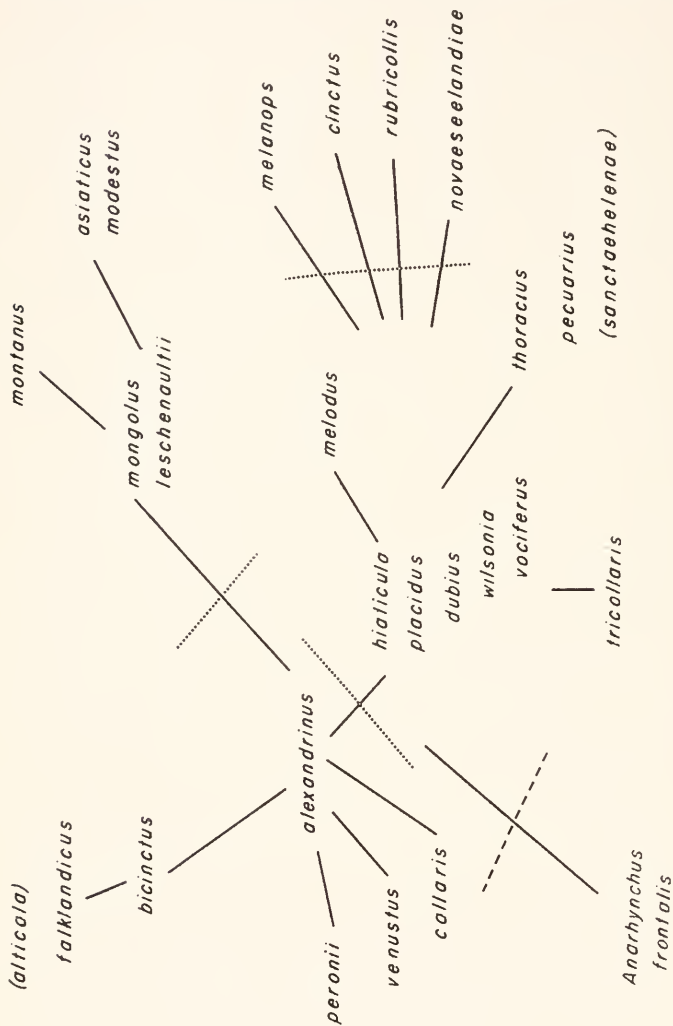


Figure 5. Dendrogram showing the relationships within *Charadrius* and the closely related *Anarhynchus*. The dotted lines separate the major sections within *Charadrius* and dashed line separates *Anarhynchus* from *Charadrius*. See text for a discussion of the relationships and evolution in *Charadrius*. (For *thoracius* read *thoracicus*.)

vary greatly and probably serve as releasers associated with both "courtship" displays and species recognition. In proposing the relationships outlined below, I have used mainly the pattern of the head and breast and to a slight extent the color of the back, but always mindful of the many dangers that exist. As in the lapwings, I doubt that it will be possible to discover the course of evolution in *Charadrius* by a study of museum skins. Nor is internal anatomy likely to provide the answer to the problem. Most probably, the solution will be supplied by a comparative study of their behavior and perhaps other techniques such as serology.

It has been impossible to determine which species or characteristics are primitive or specialized. However it is useful to designate one species as the basis for comparative purposes, and *hiaticula* has been selected for this mainly because it is so well known and not because it is considered primitive. The relationships within *Charadrius* are illustrated in Figure 5.

Group A. The typical species of the ringed plover group are *hiaticula*, *placidus*, *dubius*, *wilsonia*, *vociferus*, and *melodus*. Aberrant members are *pecuarius*, *thoracicus* and *tricoloris*.

These species are characterized by a rather well developed head and breast pattern. The African *pecuarius* and *thoracicus* have the head markings as in *hiaticula*, but a pectoral band is present only in *thoracicus*. The most aberrant member of the ringed plovers is *tricoloris* which has two breast bands but a grey throat and a somewhat different head pattern.

Charadrius pecuarius of Africa is very similar to the larger *sanctahelenae* of St. Helena. The major differences between the two forms are the larger size and the lack of the tan color on the breast in *sanctahelenae*. These two forms are similar in all other respects and there is no reason to consider them as distinct species. Thus it is proposed that they be regarded as conspecific as they generally were before Peters gave *sanctahelenae* specific rank in his "Check-list."

The Madagascan *thoracicus* is also very close to *pecuarius* and may represent an earlier invasion of Madagascar by a pre-*pecuarius* stock. Later *pecuarius* invaded Madagascar for the second time so that today the two species are sympatric. The interesting fact is that *thoracicus* has a breast band which is a "primitive"

trait in this genus; its loss in *pecuarius* represents a more advanced condition. If Africa is the original home of the species, then this is a case of a peripheral population of a species retaining a primitive characteristic. There is, however, an equally good alternative hypothesis, namely that Madagascar is the ancestral home of the species which invaded Africa and gave rise to *pecuarius* which in turn reinvaded Madagascar. If this were true, it would be the "central" population that retained the primitive character.

The ringed plovers *hiaticula* and *semipalmatus* are considered conspecific for the purposes of this paper. A fuller discussion of the status of these forms will be presented in a separate paper. To this complex belongs *placidus* which is perhaps best regarded for the present as a distinct species, but belonging to the same superspecies as *hiaticula*.

Group B. The sand plovers embrace the species *alexandrinus*, *peronii*, *venustus*, *collaris*, *bicinctus* and *falklandicus*. The sand plovers have in general a lighter colored back than that of the ringed plovers and commonly have rufous on the crown or breast. Considering *hiaticula* as our reference species, *alexandrinus* can be derived from it by a regression of the breast bands and a change from a dark to a light-brown back. *Charadrius alexandrinus*, in turn, became a world-wide species and seemed to have given rise to *peronii* in the East Indies, *venustus* in Africa and *collaris* in South America. These species are so similar to *alexandrinus* that were it not for the fact that each one is sympatric with some race of *alexandrinus*, they would be considered conspecific with it. The relationships between *alexandrinus*, *falklandicus* (including *alticola*) and *bicinctus* are more complex and will have to be discussed with some detail.

Charadrius falklandicus is found from the southern tip of South America north through Patagonia to northern Argentina. The closely related *alticola* ranges in the high Andes from northern Argentina to Peru. There is no overlap in the ranges of these two forms as given in the latest catalogues (Steullet and Deautier, 1939, pp. 565-566, 567; Hellmayr and Conover, 1948, pp. 61-64). They are very similar in size and plumage except that there are two very heavy breast bands in *falklandicus* as compared to the very faint ones of *alticola*, and that *falklandicus* loses its reddish crown and head and breast pattern in

the winter while the winter plumage of *alticola* is similar to its breeding plumage. These differences are slight compared to the overall similarities between the two birds and as there is no overlap in their ranges, there is no reason why they should not be placed in the same species. Mr. William Partridge of Buenos Aires tells me the distribution pattern of *falklandicus* and *alticola* (that is, ranging from the lowlands of Patagonia north into the Andes as far as Peru) is a common pattern of many Patagonian birds.

The mountain *alticola* is similar to *collaris* which is found in the lowlands of South America and north to Mexico. Except for a difference in size (*alticola* is larger), and the presence of a single heavy breast band in *collaris*, the two species are similar. It is possible that *alticola* is a highland representative of *collaris* that gave rise to *falklandicus*, but this is highly unlikely.

The closest relative of the subspecies *falklandicus* is *bicinctus* of New Zealand. They are almost identical except for the color of the lower breast band which is red in *bicinctus* and black in *falklandicus*. The color of the breast bands varies greatly in this group of *Charadrius* so that the contrast of a black versus a reddish band is not a very important difference. Both species lose the breast bands and head markings in the fall molt. In order to express their great similarity and as they have with little doubt descended from the same common ancestor, *falklandicus* and *bicinctus* will be considered as members of the same superspecies. The problem of dispersal over the water gap between South America and New Zealand will be discussed later.

Charadrius bicinctus has probably evolved from an *alexandrinus*-like form as shown by its similarity to that species in plumage color and pattern and by the fact that it has recently been reported to have hybridized with the Australian subspecies *alexandrinus ruficapillus*. A full discussion of the hybrid and its history can be found in Oliver (1955, p. 263). The following account has been abstracted from his discussion. Firstly, it must be mentioned that *bicinctus* breeds only in New Zealand and that part of the population migrates to Australia each winter. This could be interpreted as an indication that *bicinctus* invaded New Zealand from Australia. The migration of several European birds now breeding in Greenland and Baffinland offers

some support for this interpretation, but there is no basis for accepting it as a general hypothesis. One year at the beginning of the breeding season, a female *alexandrinus* was seen with a male *bicinctus* in New Zealand. It was assumed that it had flown to New Zealand with a returning flock of *bicinctus*. The female *alexandrinus* paired with the *bicinctus* male and nested. Both birds were seen incubating. After the first set of eggs was washed away by a flood, a second set of two eggs was laid which were later collected. One egg was infertile, the other contained a dead, partly developed embryo. Three years later another pair of female *alexandrinus* and male *bicinctus* was seen in the same area. It was implied that the female was the same one that had nested there three years before. Two chicks were raised, one of which was collected when it was a year old, and described. All facts indicate a close relationship between the two species which while they are able to interbreed, are distant enough so that the hybrids are not very viable.

It is possible that *C. alexandrinus ruficapillus* has given rise to *bicinctus* which in turn reached South America and gave rise to *falklandicus* and hence to *alticola*. On the other hand, *bicinctus* and *falklandicus* may have nothing to do with each other and the similarity between them may be due to convergence. This is entirely possible, but as they are the only species of sand plovers with two heavy breast bands, and unless a similar selection force is shown to exist to explain this convergence, it is far more likely that the two species are related. Considering all of the facts, I would prefer to read the series as *alexandrinus ruficapillus* — *bicinctus* — *falklandicus* — *alticola*, and regard the resemblance between *alticola* and *collaris* as the result of parallelism.

Peters combined the formerly accepted species *alexandrinus*, *ruficapillus*, *marginatus* and *nivosus* into a single species, an arrangement that has been generally accepted. However, there has been some doubt as to whether or not the ranges of *alexandrinus* and *marginatus* overlap. Mackworth-Praed and Grant (1952, pp. 340-342) claim that the two forms are distinct species on the grounds that their ranges overlap in the region of British Somaliland. Meinertzhagen (1954, pp. 478-479) and Chapin (1939, p. 67) agree with Peters and state that there is no over-

lap between *alexandrinus* and *marginatus* in either East or West Africa. Further study of the distribution of these forms is needed before we can be sure of their status, but for the present the best evidence is that there is no overlap in range and therefore Peters' classification will be followed.

Group C. The mountain or plains plovers, composed of *mongolus*, *leschenaultii*, *asiaticus*, *modestus* and *montanus*, have probably evolved from an *alexandrinus*-like ancestor. The rufous crown and head markings of *mongolus* are similar to those seen in some of the Far Eastern races of *alexandrinus*. The rufous breast of *mongolus* is foreshadowed in *peronii*. *Charadrius leschenaultii* is almost identical to *mongolus* and would be regarded as conspecific with that form if they were not sympatric. However, as their ranges are almost allopatric (Dementiev and Gladkov, 1951, pp. 81, 85), they are placed in the same superspecies to express their close relationship. Closely allied to this superspecies is *asiaticus* which differs from *mongolus* in its sharp white superciliary line, the black border to the posterior edge of the reddish breast and the faintness of the black line between the bill and the eye, all of which are modifications of the *mongolus* pattern. I have followed Hartert (1912-1921) and Dementiev and Gladkov (1951, p. 88) in placing *asiaticus* and *veredus* in the same species. They are extremely similar to one another in size and plumage color and as their ranges do not overlap at all, there is no basis for maintaining them as distinct species. The South American *modestus* resembles *asiaticus* except that its throat is grey, not white, and the markings on the head and breast are sharper. I have placed it in the same superspecies as *asiaticus*, in spite of the great gap between the ranges of these species, to show their relationship. The mountain plover, *montanus*, although it is a plain colored bird, shows its affinities to *asiaticus* by its white superciliary line, white forehead, and faint black line between its bill and eye. The anterior part of the crown is black as in many of its congeners.

The plains plovers are the largest and chunkiest species of *Charadrius* as well as being the species in which the head and breast pattern is developed the least. In these respects they are similar to *Pluvialis* and may be the species "connecting" the two genera.

Group D. The Australian *melanops* appears to be an aberrant offshoot of the ringed plover group for it has a black pectoral band and head markings similar to those of *hiaticula*. Its mottled back and wings are unusual for this genus and set it apart from the other species.

Group E. *Charadrius cinctus* seems to be another aberrant derivation of the ringed plovers. It has a broad black breast band that extends down the flanks to end in a series of red markings on the thighs. The solid brown of the head is continuous with the brown of the back which is very unlike the *hiaticula* pattern of a white collar separating the brown color of the head from that of the back.

Groups F and G. The two black-headed species, *rubricollis* and *novaeseelandiae*, are similar in some respects, but probably are not very closely allied. The head and foreneck of *rubricollis* are black and contrast with the white hindneck. A black band on the upper back delimits the posterior border of the hindneck. There is no breast band. Instead, a short ventral bar is present on each side of the breast. The black on the head and back is lost in the winter plumage which makes the bird look very much like a nondescript ringed plover. The forehead, sides of the face and foreneck of *novaeseelandiae* are black and separated from the brown crown by a narrow white line. There is no breast band; however, there is a thin black band about the upper back. The bill is slender and is the chief feature separating *novaeseelandiae* from the other species of *Charadrius*. Yet the difference between the bill of *novaeseelandiae* and *hiaticula* is largely bridged by some species as *melanops*, *tricoloris* and *thoracicus*.

ANARHYNCHUS Quoy and Gaimard (FRONTALIS) 1830

Included species: frontalis.

Diagnosis: The outstanding feature of this monotypic genus is its unusual bill which bends sharply to the right at its midpoint. The angle of the bend is about 20 degrees and is already present in the chick. The dorsal surface is grey; underparts are white with a black breast band of even width throughout. For a time it was believed that the band was wider on the left side; however, this is not so. The tail is grey, sometimes with lighter edges. The flight feathers are dark grey with a faint wing bar;

the rest of the wing is lighter grey similar to the back. In the fall molt the black breast band and head marks are lost. The immature bird is similar to the adult winter plumage. The wrybill breeds inland in the shingly (rocky) river beds; the nest is placed among the rocks (Oliver, 1955, p. 269). During the rest of the year it is found on mud and sand flats along the coast. Habits and behavior are in all respects like those of *Charadrius* (Stead, 1932).

Range. Resident in New Zealand; breeds on South Island and winters along the coast of North Island.

Remarks: In spite of its remarkable bill, *Anarhynchus* is a poorly marked genus. In fact, save for structure of the bill which is unique among birds, there would be no basis for separating *Anarhynchus* from *Charadrius*. Because of the importance of the bill in the differentiation of *Anarhynchus*, an inquiry into the feeding habits of the wrybill and the functional significance of the bend in the bill would be most desirable.

The habits of the wrybill have been discussed in a number of papers (Potts, 1871, pp. 93-97; Hutton and Drummond, 1923, pp. 216-218; Smith, 1926, p. 41; Stead, 1932; Oliver, 1937; and summarized in Oliver, 1955, p. 269). The habitat and distribution of the wrybill which are vital to the problem of the function of its bill are described in the above papers, especially by Stead, and also by Sibson (1943), and Urquhart and Sibson (1952). Yet the feeding habits have never been adequately described. According to Potts (p. 96) the bend in the bill would aid the bird in capturing insects that are found abundantly under the water-worn rocks of the river beds of its breeding grounds. Stead's conclusions (pp. 91-92) are somewhat colored by his beliefs, so that, although his evidence supports Pott's earlier statement, he does not believe that the wrybill gains any advantage from its deflected bill. Smith (p. 41) says: "in North Island, where the bird migrates in the winter he had observed it sweeping the wet sands with a remarkable scythe-like action of its bill for some minute food supply." Despite the fact that the wrybill is a common and easily observed bird, this constitutes our entire knowledge of its feeding habits. A complete description of its feeding habits on both the breeding and wintering

grounds is sorely needed. The use of motion pictures and a statistical approach to the problem would be desirable.

Even though the evidence is poor, there is enough to indicate that *Anarhynchus* utilizes the bend in the bill in two ways. When it is on its rocky breeding grounds, the bend is advantageous in obtaining insects found under the rocks. On the mud flats of its wintering grounds, it may make use of the crook in the sweeping motions described by Smith. Until we have careful observations, these suggestions are the best that can be offered. However, it is certain that the bill is used in some special way(s); there had to be some selection force(s) responsible for the evolution of this peculiar bill.

The second aspect concerns the anatomical features of the skull and how they became modified with the change in the shape of the bill and feeding habits. It would be most interesting to see if the asymmetry of the anterior part of the bill is reflected in the hind part of the skull. A thorough study of the functional anatomy and evolution of the deflection in the bill of *Anarhynchus* should provide a most fascinating study of adaptation in the bill of birds.

Related to the structure of the bill is the problem of whether this species should be given generic rank. Aside from its bill, the wrybill agrees with *Charadrius* in all respects. It has with little doubt evolved from some member of *Charadrius*, and except for the shape of its bill, would be placed in that genus without hesitation. The handling of cases in which a species differs from its nearest relatives in a single character, no matter how remarkable, was discussed in connection with *Cochlearius* in my revision of the herons (Bock, 1956, pp. 31-35). *Anarhynchus* has not yet given rise to any new radiation of forms and may well represent an evolutionary dead-end. I do not consider *frontalis* markedly different from *Charadrius* and it is with much hesitation and reluctance that it is kept in a separate genus, but done only to point out the truly unique structure of its bill. However if the generic limits in the plovers are further broadened, this genus will almost automatically have to be merged with *Charadrius*.

EUDROMIAS C. L. Brehm (MORINELLUS) 1830

Synonymy: *Oreopholus* Jardine and Selby, 1835 (*ruficollis*); *Morinellus*

Bonaparte, 1856 (*morinellus*).

Included species: morinellus and ruficollis.

Diagnosis: Medium sized plovers with medium to long bills. The back is mottled, but unlike that of *Pluvialis*. The crown of the adult is solid brownish and bordered by a white superciliary line. The breast is uniformly colored, reddish or tan. The wing is similar to the back in color and pattern and without a wing stripe. Winter plumage (*morinellus* only ?) lacks the color of the underparts of the breeding plumage. The immature is similar to the winter plumage of the adult.

Range: *E. morinellus* breeds in the tundra and mountains of northern Eurasia and winters in the Mediterranean region and southern Asia. *E. ruficollis* is a permanent resident in the mountains and plains of southern South America.

Remarks: The grouping of these species into one genus may well be artificial. However the two species agree in many points of color pattern that are not seen in any other plover. The large gap between the ranges of the two species is a problem, but not an insurmountable one when compared to the many disjunct ranges in other genera. The number of similarities that exist in these two species makes it reasonable to regard them as congeneric unless additional evidence should prove otherwise.

PLUVIANELLUS G. R. Gray (SOCIALIS) 1846

Included species: socialis.

Diagnosis: This medium-sized plover has a solid grey back and white underparts with a broad grey breast band in the female while the breast of the male is mottled grey. The wings are dark grey with a broad white wing stripe much like the wing stripe of *Vanellus*. The central tail feathers are dark grey; the lateral ones are dirty white. The bill is rather flattened laterally for a plover and is sharply pointed. In some ways the bill resembles that of the turnstones. The habits of this species are given in Goodall *et al.* (1951, pp. 216-217) and seem to be like those of the rest of the charadriine plovers.

Range: Found only in Tierra del Fuego.

Remarks: *Pluvianellus* is a nondescript and rather strange plover. Nothing that can be seen in a museum skin gives any clue to its relationships. I have not seen any anatomical material of

this species, nor has its anatomy ever been described. Most of its features, except for the broad wing stripe, are more charadriine-like than vanelline-like, but are still not very convincing. I have considered it as allied to the *Charadrius* group on the basis of past usage rather than on any strong evidence, and should like to emphasize that much more must be known about the anatomy and behavior of this plover before we can be reasonably sure of its position.

Genera Incertae Sedis

PHEGORNIS G. R. Gray (MITCHELLII) 1846

Included species: mitchellii.

Diagnosis: A small bird, about the size of *C. hiaticula*. The head is dark brown with a narrow white band across the forehead, continuing around the sides as a supereiliary line and completing the circuit about the rear of the head. The back of the neck is reddish-brown while the back is dark brown. Chin and throat are black, the rest of the underparts are barred with black and white transverse strips. The tail is dark brown except for the lateral feathers which are white with dark bars as seen in the tail of many sandpipers (*e.g. Tringa solitaria*). Wings are dark brown with the secondaries tipped with white. The bill is quite long and thin compared to that of the plovers.

Range: High Andes from Peru south to central or southern Chile.

Remarks: The relationships of this genus are still obscure and there are good reasons to doubt that it is even a plover. Seebohm placed it with the sandpipers (Scolopacinae) and included *cancellatus* (= *Aechmorhynchus cancellatus* and *A. parvirostris* of Peters) and *leucopterus* (= *Prosobonia leucoptera* of Peters) in the same genus. Sharpe kept the three species in the Scolopacidae *sensu stricto*, but separated them into three genera. In his first paper on plovers, Lowe (1922, p. 491) stated that he did not have anatomical material of *mitchellii* and hence did not commit himself as to its systematic position. However in his major work (1931b, p. 743) he placed *Phegornis* in the Charadriidae *sensu stricto* on the basis of its color pattern (no elaboration given) and the nature of its maxillo-palatine strut which

is illustrated on page 769 (see Figure 6). The difference between the plovers and the sandpipers in this structure, according to Lowe, is that in the plovers the maxillo-palatine strut meets the jugal bar at right angles, while in the sandpipers the strut runs forward from the maxillo-palatines to meet the jugal bar at a rather sharp angle. In addition to the differences given by Lowe, the maxillo-palatine strut of the plovers fuses to the jugal bar

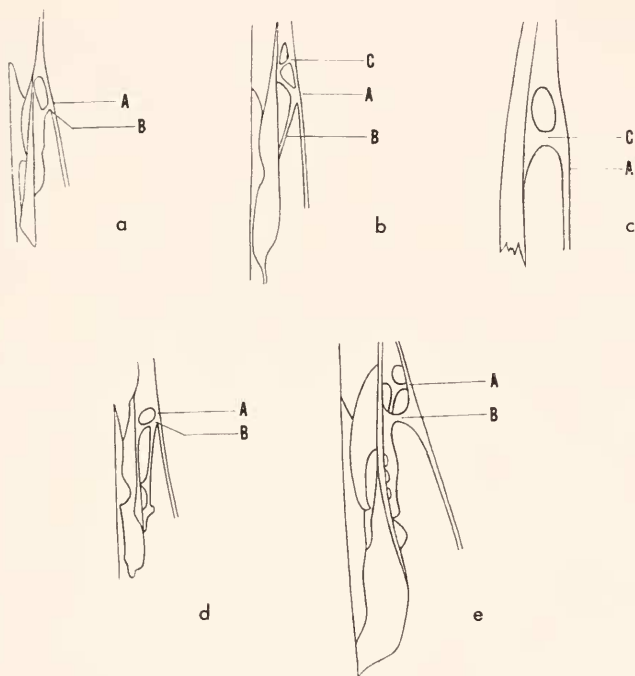


Figure 6. Ventral view of the left side of the palate of a) *Erolia*, b) *Tringa*, c) *Phegornis* (after Lowe, 1931b, p. 769), d) *Arenaria*, and e) *Pluvialis* to show the nature of the maxillo-palatine strut. The anterior end of the palate is at the top, midline is to the left. The labeled structures are: A) the point of junction between the jugal bar and the lateral ramus of the nasal bone (not shown in the drawing), B) the maxillo-palatine strut, and C) an unnamed strut anterior to the maxillo-palatine strut. Figures are twice life size.

at a point posterior to the junction of the jugal bar and the lateral ramus of the nasal. In the sandpipers, on the other hand, the junction of the strut is at a point where the lateral ramus of the nasal fuses to the jugal bar. This is quite evident in Lowe's drawings but is not mentioned by him in the text. In the plovers, the maxillo-palatine strut is always as described by Lowe. The sandpipers, however, exhibit a considerable amount of variation which was appreciated and described by Lowe. Usually the strut is as described above or a minor variation of it. But in some genera, notably *Tringa* and its allies, the strut meets the jugal bar almost at a right angle at a point slightly posterior to the junction of the lateral process of the nasal bone and the jugal bar. In spite of its variation in the sandpipers, the nature of the maxillo-palatine strut seems to be a good means of separating the plovers from the sandpipers. In Lowe's drawing of *Phegornis* on page 769, the process labeled as the maxillo-palatine strut, while it does meet the jugal bar at right angles, is anterior to the junction of the jugal bar and the lateral ramus of the nasal, not posterior as in all other plovers. Also the more dorsal parts of the palate included in the drawings on pages 735 and 736 illustrating the strut in other plovers and sandpipers seem to be omitted in this plate. If the drawing of *Phegornis* is compared to the one showing the palate of *Tringa* (Figure 6, and see also Lowe, 1931b, p. 375, fig. b), the bone marked as the maxillo-palatine strut in *Phegornis* seems to correspond to an unnamed process in *Tringa* which is anterior to the maxillo-palatine strut and which meets the jugal bar at right angles, but which is just anterior to the junction of the jugal bar and the lateral bar of the nasal bone. Because of these differences, I would hesitate to definitely label the strut shown by Lowe in his drawing of *Phegornis* as the maxillo-palatine strut seen in other species of plovers and sandpipers, but instead suggest that it corresponds to the above mentioned, but unnamed strut in *Tringa*. I have not seen any anatomical material of this species and until I do, I cannot make a more definite statement about the condition of the maxillo-palatine strut in *Phegornis*.

Lowe (1927; 1931 a, b) studied the anatomy of *Aechmorrhynchus cancellatus*, one of the species considered closest to *Phegornis* by Seebohm. He concluded that *Aechmorrhynchus* was a

sandpiper and most closely related to the group that he called the Limosinae (*Bartramia*, *Numenius*, *Limosa*, etc.). In regard to the maxillo-palatine strut in this species, Lowe said only that: "the maxillo-palatine region seems to conform to the arrangement seen in the curlews" (1927, p. 129), but further on he says that this region was badly decalcified, thus making the determination of the morphological features very difficult.

According to Lowe, the color of *Phegornis* agrees with that of the plovers, but did not cite any definite points of resemblance. The barred underparts and tail (underside and edges) of *Phegornis* match the plumage of some sandpipers and are quite unlike any plover. The pattern of the head is, however, similar to that found in many charadriine plovers. It should be stressed that as a general rule, it is unsafe to determine the family status of a bird on the basis of its color pattern. In *Phegornis* the taxonomic implications of the plumage color and pattern are certainly unclear.

Phegornis is found along mountain streams in pairs or singly where it walks on the rocks looking for aquatic animals under the algae that cover the rocks. It is protectively colored, silent and tame so that it is difficult to see until it flushes at the last possible moment and flies off with strong wing beats. The nest is a depression in the grass, not far from water. This account taken from Goodall *et al.* (1951, p. 218) is the extent of our knowledge of this species and is of no help in discovering its true position.

Peters and other recent workers follow Lowe and assign *Phegornis* to the Charadriinae *sensu stricto*. No one has studied the anatomy of this species since Lowe and indeed we are still completely ignorant of its morphology. While I believe that future work will prove that *Phegornis* belongs to the Scolopacinae, perhaps allied to *Aechmorhynchus* and *Prosobonia*, there is no evidence at present to support this belief. I must also emphasize that there is at present no reason other than past usage to retain *Phegornis* in the plovers. However, the most practical solution is to keep *Phegornis* in the Charadriinae until evidence proves otherwise, but to remember that its true affinities are still unknown.

PELTOHYAS Sharpe (AUSTRALIS) 1896

Included species: australis.

Diagnosis: The upper parts of this medium-sized bird are mottled brown, much like those of *Eudromias*. The throat, breast and belly are tannish, the lower breast is reddish brown, and the under tail coverts whitish. The white forehead is bordered behind by a black bar extending between the eyes and continued below the eye as a short vertical bar. There is a black breast band that is continuous about the back. The breast band extends down the mid-ventral line as a narrow streak as far as the lower breast. The wings are similar to the pattern of the back with no wing bar. The tail is brownish with lighter outer tail feathers. The immature is like the adult, but lacks the black markings on the head and breast. The hind toe is lacking. The bill has an expanded distal portion, and while it is slightly pointed, it is no more so than the bill of *Pluvianellus*.

Range: Australia.

Remarks: This puzzling genus was originally described as a species of *Eudromias* by Gould and placed in that genus or *Charadrius* until Sharpe placed it in a separate genus and subfamily of the Charadriidae *sensu stricto*. Seebohm included *australis* in *Charadrius* near *C.* (= *Eudromias*) *morinellus*, but was not sure of its proper position as indicated by his remark (1888, p. 110): "It is difficult to say which it most resembles, *Charadrius hiaticula*, *Charadrius morinellus* or *Cursorius bicinctus*, but its resemblance to the latter is probably an example of analogy rather than affinity."

Mathews (1913-1914, pp. 335-336) placed *Peltohyas* in the Glareolidae on the basis of the shape of the bill, the scutellation of the tarsus, and the flattened nature of the claws. Lowe (1931b, p. 771) listed several anatomical characters such as the thigh muscle formula, the patagial wing muscles, the feather tracts of the neck, and some aspects of the skull and vertebral morphology in which *Peltohyas* agrees with the glareolids and not with the charadriids. A number of these characters are those given by Gadow (1893, pp. 195-203) and Beddard (1898, pp. 336-350) to separate the two groups and thus may be of considerable taxonomic importance.

Externally, *Peltohyas* in all respects resembles the plovers. In plumage it is closest to *Charadrius* which it resembles in the head markings, breast band and tail pattern, and does not match in any way the plumage of any species of the Glareolidae. The bill is that of a plover and is completely unlike the arched, pointed bill of the glareolids. While the scutes of both the anterior and posterior surfaces of the tarsus are rectangular, they are not like those of the glareolids, especially the scutes of the plantar surface, but rather more like those of some species of *Vanellus* or *Eudromias ruficollis*. A number of species of plovers have rectangular scutes on the front surface of the tarsus, but at best the scutes of the plantar surface are hexagonal. The middle claw of most genera of the Glareolidae is pectinate (lacking in *Stiltia* and rudimentary in *Rhinoptilus*), but while the claws of *Peltohyas* are flattened, the middle claw is not pectinate.

In view of the strongly conflicting evidence — the external features being charadriine-like while some of the features of the internal anatomy (as reported by Lowe) agree very closely with the Glareolidae — *Peltohyas* must be placed with the other genera of uncertain position. A careful comparative anatomical study of *Peltohyas* and the Charadriinae and the Glareolidae is needed before it can be assigned to the proper family.

The Turnstones ('Arenariini')

The genera *Arenaria* and *Aphriza* may be thought of as a tribe of shorebirds of uncertain affinities, "Arenariini." They have been placed either in the Charadriinae *sensu lato* or in the Scolopacinae *sensu lato*, but a convincing argument for either proposal has never been given. Most authors include the turnstones in the plovers, basing their action on such external features as the shape of the bill and the plumage pattern. At present, this is the most widespread opinion. Lowe, on the other hand, cites several features of the skull in which the turnstones agree with the Scolopacinae *sensu lato* and not with the Charadriinae (see Lowe, 1931b, p. 747). These characters are: the type of maxillopalatine strut (see Figure 6, and for a discussion of this structure, see above, p. 81), the nature of the articulation of the quadrate with the skull, and lastly the shape of the mandibular articular surfaces of the quadrate. I have compared skulls of

Arenaria and *Aphriza* with skulls of a number of genera of plovers and sandpipers and thus far have confirmed Lowe's earlier findings and conclusions. The condition of the supraorbital rims in *Arenaria* is illustrated in Figure 1e. The rims do not resemble those of any of the plovers and are similar to those of sandpipers in the narrow shelves of bone. Within the sandpipers, Lowe places the turnstones closest to the eroliine group and proposes the following "evolutionary sequence": *Erolia* (perhaps more definitely *E. maritima* or *E. ptilocnemis*) — *Aphriza* — *Arenaria*, a reasonable hypothesis that deserves serious attention. However, Lowe's works need to be checked before they can be accepted and until the anatomy of the turnstones is further studied and compared with that of the plovers and the sandpipers, they must be regarded as a group of doubtful affinities. Yet for the present there is better evidence for placing the turnstones in the *Scelopacinae sensu lato* and they will be considered as members of this group for the purposes of this paper. If future work shows that the turnstones are in reality related to the plovers rather than to the sandpipers, the present evidence indicates that they probably would have to be considered as a group distinct from the species studied in this paper; perhaps the two groups would be best regarded as separate tribes.

Zoogeographic Considerations

A careful examination of the ranges of closely related species of plovers reveals a number of interesting zoogeographic problems. For example, some members of the same species or super-species are separated by ocean gaps of 1000 to 5000 miles. Equally interesting are the species that are confined to a small area somewhere in the southern tips of the southern land masses. There are enough problems of general zoogeographic interest to warrant a full discussion of some aspects of the distribution and dispersal of the plovers. In a recent paper, Larson (1957) discusses the past and present distribution of the North Temperate and Arctic shorebirds, including the plovers, to which the interested reader is referred.

The present day center of distribution for the lapwings is Africa and for the charadriine plovers, the Holarctic region. All Arctic species migrate south in the winter often as far as

the southern tips of South America, Africa and Australia. Many of these species make extremely long flights (1000 miles or more) over the ocean; an excellent example is the flight of the golden plover (*Pluvialis dominica*) from Nova Scotia to South America or from Alaska to Hawaii. They may rest on long flights by settling on driftwood (Nicholson, 1928, pp. 126-127), or by swimming if they are forced to (Cottam, 1928, and numerous other reports). Except for *Phegornis*, which may not even be a plover, most species are highly gregarious or at least occur in small flocks. Lastly, there are a few records of northern species breeding in their winter range: *P. dominica* in New Zealand (Robson, 1884), which apparently bred in its winter plumage, nest found on January 9, 1883, eggs hatched two days later; and the chick of *C. leschenaultii* has been found in the region of the Red Sea (Archer and Godman, 1937, pp. 384-385, and Meinertzhagen, 1954, pp. 482-483). It should be pointed out that some species of plovers are wintering in the temperate areas of the Southern Hemisphere at a time when the day length is increasing and reaching a maximum in these regions. Nothing is known of the annual cycle of these species and its correlation to day length, and especially the possible effects of wintering in the south temperate zone.

Apparently for plovers, ocean gaps are not important barriers to successful colonization of new areas. Two examples of recent invasions may be cited. In 1927, during the winter, large flocks of the European lapwing, *V. vanellus*, flew from England to Newfoundland and Labrador when they missed their course in a storm (Spencer, 1953, p. 88). *Vanellus miles novachollandiae* has recently successfully invaded New Zealand from Australia (Oliver, 1955, p. 270).

Thus the three species of lapwings found in South America had with little doubt come from the west coast of Africa. The two species *chilensis* and *resplendens* represent one invasion, and the third species, *cayanus*, represents a separate invasion. *Charadrius alexandrinus* has probably also travelled over this route.

The close relationship between *Pluvialis obscura* of New Zealand and the Arctic *apricaria-dominica* and *squatarola* can best be explained by regarding *obscura* as descended from a group

of individuals of some species of *Pluvialis* that remained in New Zealand to breed. The old nesting record of *dominica* in New Zealand offers some support for this hypothesis.

Charadrius bicinctus (New Zealand) and *falklandicus* (South America) belong to the same superspecies, but their ranges are separated by many thousands of miles of open ocean. It is possible that the invasion was direct from New Zealand to South America. There is, however, another possibility that may be more likely. It is well known that at times in the past, Antarctica was not always covered with ice (Axelrod, 1952 a, b). If the ice at the edges of the Antarctic Continent melted and a tundra-like vegetation developed, there is no reason why plovers should not have bred there and migrated north in the fall. If this is true, then *bicinctus* could have reached South America by way of Antarctica. More likely *falklandicus* and *bicinctus* differentiated from each other in Antarctica, one migrating north to South America and the other to New Zealand and Australia. This may well be the explanation of the relict nature of the species (ten in number) of Southern Hemisphere plovers that are found today breeding in a small area in the very southernmost tips of the southern land masses. It is of interest that the relict plovers are all related to the present-day Arctic species and that there are no plovers confined to the Cape of Good Hope region of Africa.

The gaps between the ranges of *Charadrius asiaticus* and *modestus* or between *Eudromias morinellus* and *ruficollis* are the largest of any that exist in the plovers. In both cases it is a gap between northern Asia and the southern Andes. But even here, it could be explained by invasion and perhaps a partly relict nature of the southern species.

It is hoped that these considerations of the migration and dispersal habits of the plovers have shown that there is nothing in the proposed classification of the Charadriinae that is in conflict with currently accepted principles of zoogeography.

History and Future Studies

The shorebirds, including the plovers, being conspicuous birds became well known early in the history of ornithology. A brief survey of the dates of the original descriptions shows that less

than half a dozen species were discovered in the past century and all were known before the turn of the century. It is quite safe to say that no species of plovers remains to be discovered, but much must still be done before we understand the geographic variation and status of many species (*e.g.* *Charadrius hiaticula*).

Much has been published on the generic and suprageneric relationships of the Charadriinae; however, few of the conclusions have stood the test of time. The same is true of the past anatomical work. While it is hoped that the delimitation of genera proposed in the present study is reasonable, little can be said of their relationships and evolution. We cannot even set limits to the Charadriinae or determine whether several genera such as *Phegornis*, *Peltohyas*, *Aphriza* and *Arenaria* belong to this subfamily or to some other group. Our knowledge of the anatomy of these groups is almost nonexistent so that a good comparative study of the anatomy of the entire shorebird group is sorely needed. Perhaps after this is done, we may gain some understanding of the evolution of the Charadriinae and their position in the Charadriidae.

Behavior was briefly mentioned several times in the discussions, but never gone into fully. Despite the fine work that has been done on the behavior of several species (Rinkel, 1940; Laven, 1940; Laven, 1941; Deane, 1944; Williamson, 1948; Simmons, 1952, 1953, 1955; and Smith and Hosking, 1955), the comparative ethology of the plovers is still in its beginnings and of no help to our understanding of the specific relationships of the plovers at this time. Yet all indications point to the fact that the relationships within the large genera, *Charadrius* and *Vanellus*, and perhaps even between the genera will be understood only after their behavior is well known, so that the need and desirability of behavioral studies comparable to those done on the ducks, gulls and terns cannot be urged too strongly.

A knowledge of the ecology, even a rough indication of their habitat, is necessary for a proper understanding of several features of the anatomy and plumage and here again careful studies are not available and are much needed.

It can be seen that while much work has already been done, our knowledge of the biology of the plovers must be greatly increased if we hope to understand the relationships and evolution

of this group. This review must then be thought of, not as a definitive study, but rather as a preliminary work with the hope of clearing the path for future studies.

Summary

The structure and variation of the skull of the plovers were studied. It was shown that the degree of ossification of the supra-orbital rims is strongly correlated with the size of the nasal glands and hence with the salinity of the water, and is of no taxonomic value. Some other features of the skull were also studied.

The important earlier works on the classification and anatomy of the Charadriinae were discussed, especially those of Lowe upon which much of the current accepted classification is based. It is shown that Lowe's interpretations of the morphology of the skull, color and color pattern are at variance with many of the observed facts and with many of the ideas and principles of evolution and classification. Any classification of the plovers resulting from these interpretations would, therefore, be highly artificial.

In addition to the skull, the major characters studied were the hind toe, the wattles, the wing spur, the color and color pattern of the plumage, and the osteology. Each character is described and its variation and possible evolution within the subfamily, and its value in the proposed classification is discussed. The importance of the habitat is mentioned.

A new classification of the plovers, based on a comparative study of the above mentioned characters, is presented. The plovers, following Mayr and Amadon, are considered as a subfamily Charadriinae of the Charadriidae. The subfamilies Charadriinae and Vanellinae of Peters are dropped and the 56 recognized species are placed in 6 genera as compared to the 61 species and 32 genera of Peters. No new species or genera are proposed. A diagnostic description is given for each group within the Charadriinae, but not for the subfamily as a whole. The status of several genera remains uncertain. *Plegornis* is retained in the plovers only on the basis of past usage, but it is believed that more study will prove it to be a member of the Scolopacinae. *Peltohyas* may belong either to the Charadriinae or to the Glareolidae; at present its status is very uncertain. The turnstones and surf-birds, *Arenaria* and *Aphriza*, are for the purposes of this

paper considered as sandpipers, but their position is still doubtful. A discussion of subspecies lies outside the scope of this review.

A brief mention of the zoogeographic implications of the proposed classification is given. Lastly, a brief summary of past investigations of the group including an outline of the largest gaps in our knowledge of the biology of the plovers is presented.

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